

## PROSERPINOID LAND SNAILS AND THEIR RELATIONSHIPS WITHIN THE ARCHAEOGASTROPODA

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### ABSTRACT

The classification of the proserpinoid land snails is reviewed. Two families are recognized, Proserpinidae and Ceresidae new family. The Proserpinidae are confined to the West Indies and include a single genus with eight extant species. The Ceresidae are currently known from Mexico and South America and contain five genera and thirteen species. The Ceresidae are a family of terrestrial diotocardian Archaeogastropoda that have two functional auricles, are holopod, lack an operculum and have a lamella barrier within the aperture. The Proserpinidae are more specialized, with a single auricle and an aulacopod foot, but also lack an operculum and have an internal barrier.

On the basis of morphological data two families of prosobranch snails can be derived from the Ceresidae: the Proserpinidae and the Helicinidae. The Helicinidae have a single auricle, a holopod foot, an operculum, and lack a lamellar barrier. The operculum is a derived structure that more effectively closes the aperture to intruding objects than does the lamellar barrier in the ancestral groups. The relationship between the Ceresidae and the Helicinidae is clear on the basis of known anatomical data. The relationship between the Proserpinidae and the Helicinidae is less clear. The Proserpinidae and the helicinid subfamily Vianinae have similar radulae which are divergent from the basic type that occurs in other Helicinidae and the Ceresidae. Other anatomical characteristics of the Vianinae are typically helicinid. Probably the similar radulae of the Proserpinidae and the Vianinae are due to convergent evolution for similar trophic activities and do not reflect a close relationship between the two groups.

The families Ceresidae, Proserpinidae and Helicinidae comprise the new superfamily Helicinacea. The Hydrocenidae, which frequently are placed in close association with the Helicinidae, are herein placed in a separate superfamily, Hydrocenacea.

The Helicinacea is postulated to have evolved from a primitive marine diotocardian ancestor, but not from the Neritacea.

### INTRODUCTION

The classification of proserpinoid land snails into family and subfamily units has satisfied few malacologists who have worked with them. The first species to be described were thought to be pulmonate land snails because of the lack of an operculum and the presence of a lamellar barrier within the aperture, broadly similar to the lamellar barrier that occurs in several families of pulmonate land snails. Gray (1856) and Bland (1863) established the relationship of proserpinoids to the prosobranch Helicinidae. Baker (1922, 1926b) and Thiele (1931) gave additional data on the radula, and affirmed the relationship of the proserpinoids to the Helicinidae.

Only a single review of the proserpinoids has been published within the last century. Boss & Jacobson monographed the West Indian species (1975a) and gave an overview on the classification of mainland taxa (1975b).

They treat the group as a subfamily, Proserpininae, of the Helicinidae and recognize two genera, *Ceres*, confined to Mexico, and *Proserpina*, including all other mainland and West Indian species. Other authors (Thiele, 1931: 89-91; Wenz, 1940: 447-448; Keen, 1960: 1287-1288) gave various schemes of generic classification but did not treat the species.

The recent discovery by the author of two new species of *Proserpina* in Hispaniola has led to the anatomical examinations of two species and a more critical examination of the shells of other described mainland species. These studies necessitate a reevaluation of proserpinoid classification. Although the anatomical information is, unfortunately, limited to two species, enough data on the anatomy of the Helicinidae are available to give substantial weight to the anatomical criteria used for classification in this paper. This paper consists of three sections. The first presents ana-

tomical data on some species. The second section deals with the phylogeny of the proserpinids and related families. The third section deals with taxonomic observations on proserpinoids and a synopsis of the species.

## MATERIALS AND METHODS

The anatomical information presented below is based upon two species, *Ceres nelsoni* Dall and *Proserpina nitida* Sowerby. Also included are published observations on the radula of *Ceres salleana* Gray, *Linidiella swifti* (Bland), and *Proserpina (Despoenella) depressa* (Orbigny). Specimens of *Ceres nelsoni* were collected at various localities in wet forests over limestone substrates in San Luis Potosí, Mexico (see *Distribution* under *C. nelsoni*). Most (UF<sup>1</sup> 24405, UF 24406) were collected by James Reddell, Texas Tech University, while he conducted speleological studies. These specimens were dropped live into 70% isopropanol. One male (UF 24091a) was collected by the author. It was narcotized in water with menthol crystals, killed in Bouin's fixative, and preserved in 70% isopropanol. Forty-three specimens of *Proserpina nitida* were studied. These were collected by Glenn Goodfriend at 1.3 mi S. Clarmont, St. Ann Parish, Jamaica, on 1 November 1976 at night. These were drowned in water and preserved in 70% isopropanol.

**Methods:** Dissections were made under 70% isopropanol. The mantle collar and mantle were removed dorsally to reveal the internal arrangement of the pallial organs, the pallial gonoduct, and the lower intestine. Next, the reproductive system was teased free from other organs and removed. Then the dorsal body wall over the head and nape was opened to reveal the central nervous system and the anterior digestive system. Radulae were cleaned in 1% KOH. Radulae for photomicroscopic study were stained with 10% Harris's Haematoxylin. Radulae were also studied with a Cambridge Mark II scanning electron microscope. Reproductive systems were serial sectioned at 10  $\mu\text{m}$  and stained with 10% Harris's Haematoxylin.

The nervous systems of *Ceres* and *Proserpina* do not differ from those of the Helicinidae. Thus they are not described in the anatomical section, but are discussed later.

**Terminology:** The Helicinacea differ from

other Prosobranchia in the structure of the posterior portion of the pallial gonoduct and adjacent organs, for which special terminology has been used (Thiele, 1902; Bourne, 1911; Baker, 1925, 1926a).

**V-organ:** A peculiar topological configuration formed by the lower end of the primary oviduct and the adjacent portion of the pallial oviduct, which combine to form a thick-walled V-shaped structure. The pallial portion is called the *pedicel*.

**Accessory sperm sac:** A small bulb (seminal receptacle II?) on the pedicel. Baker (1925) stated that it probably is homologous with the common reno-pericardial-gonadic duct of ancestral gastropods.

**Provaginal sac:** A thin-walled sac on the side of the vagina just above the vaginal opening, and is derived from the vestigial right kidney of ancestral rhipidoglossans (Thiele, 1902; Baker, 1925).

**Reception chamber:** A voluminous chamber lying between and connecting the pedicel, the pallial oviduct, and the vagina; term *seminal receptacle* is used in this paper to comply with other prosobranch terminology; however, the bursa copulatrix, provaginal sac, reception chamber, and accessory sperm sac all receive spermatozoa, so the function of the reception chamber is not unique as a receptacle (Baker, 1925, 1926a).

**Hypobranchial duct:** Generally a thin-walled duct leading from the hypobranchial gland into the mantle cavity; in the Helicinidae the vagina opens inside the duct, thus incorporating the structure into the reproductive system. Bourne (1911) and Baker (1925, 1926a), described the histology of the gland and duct.

**Ureter:** Equivalent to *renal papilla* in other Prosobranchia, and not ureter as occurs in the Pulmonata. Renal papilla is used in this paper.

**Aulacopod-holopod foot:** The side of the foot in the Proserpinidae is circumscribed by a continuous groove originating from the anterior mucous groove and demarcating a narrow band of tissue bordering the sole. This groove is similar to the aulacopod foot of some Pulmonata. The holopod foot refers to the absence of such a demarcating groove. These terms are used as adjectives in this paper and no homology with the Pulmonata is implied.

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ANATOMY OF CERES AND PROSERPINA

*Ceres nelsoni* Dall

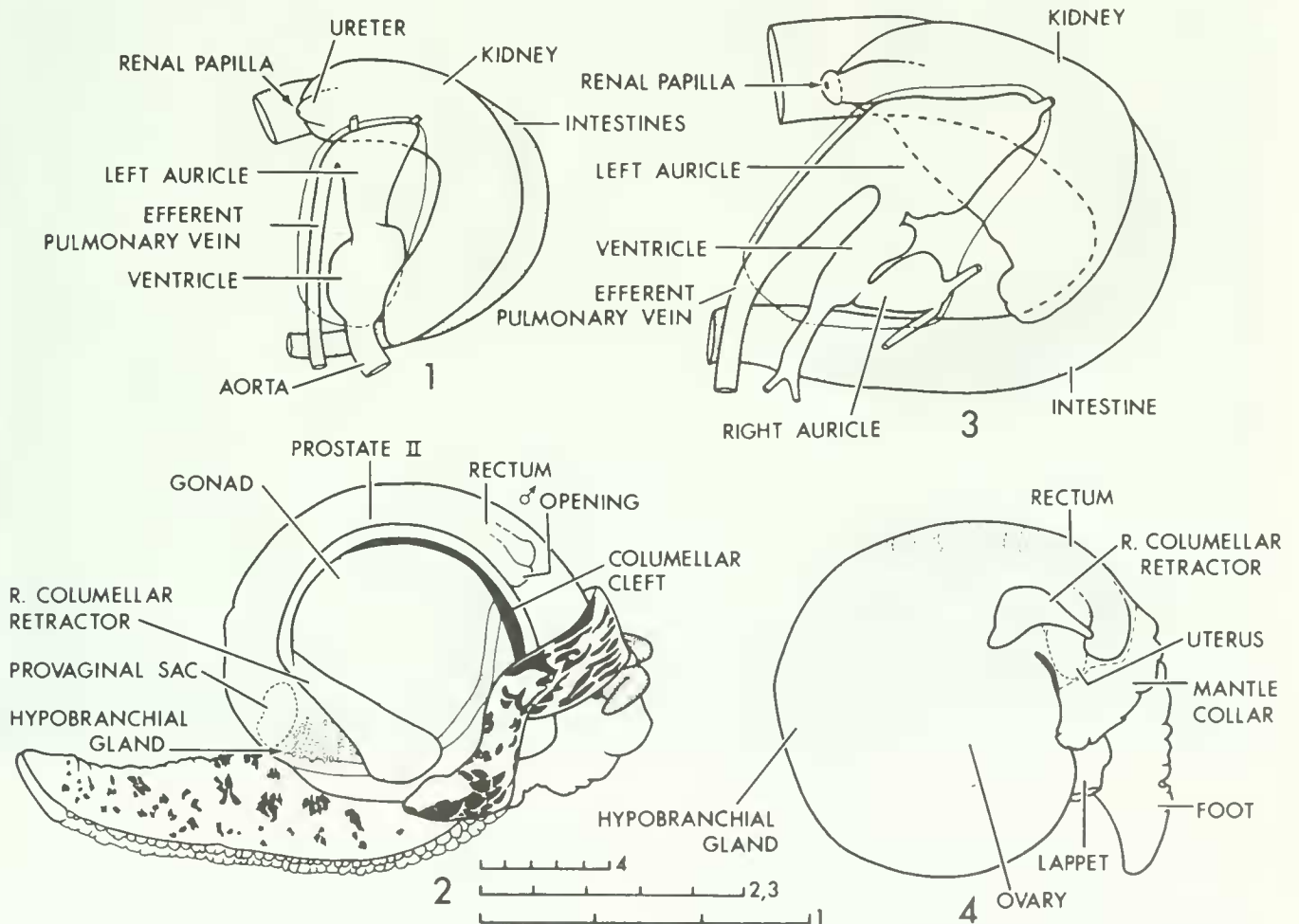
The following observations are based upon twelve preserved specimens. All illustrations are based upon specimens from UF 24405 (see species account for data).

**External anatomy:** Foot holopod, moderately long, broadly spatulate; broadly triangulate in cross-section posteriorly, and bearing long dorsal keel; caudal pore absent. Sole undivided longitudinally. Snout projecting beyond it anteriorly; deep anterior mucous groove along anterior margin of foot extending posteriorly on each side for distance about equal to half the width of sole; sides of foot and snout diffusely mottled with black. Tentacles long, slender and black with black bar connecting them across nape. Eyes on outer side of tentacles just above their base. Mantle collar white with diffuse gray along anterior edge. Collar completely surrounding body and bearing narrow, free lappet that is confined dorsally within shell; ventrally the lappet expands posteriorly to form thin pad upon which shell

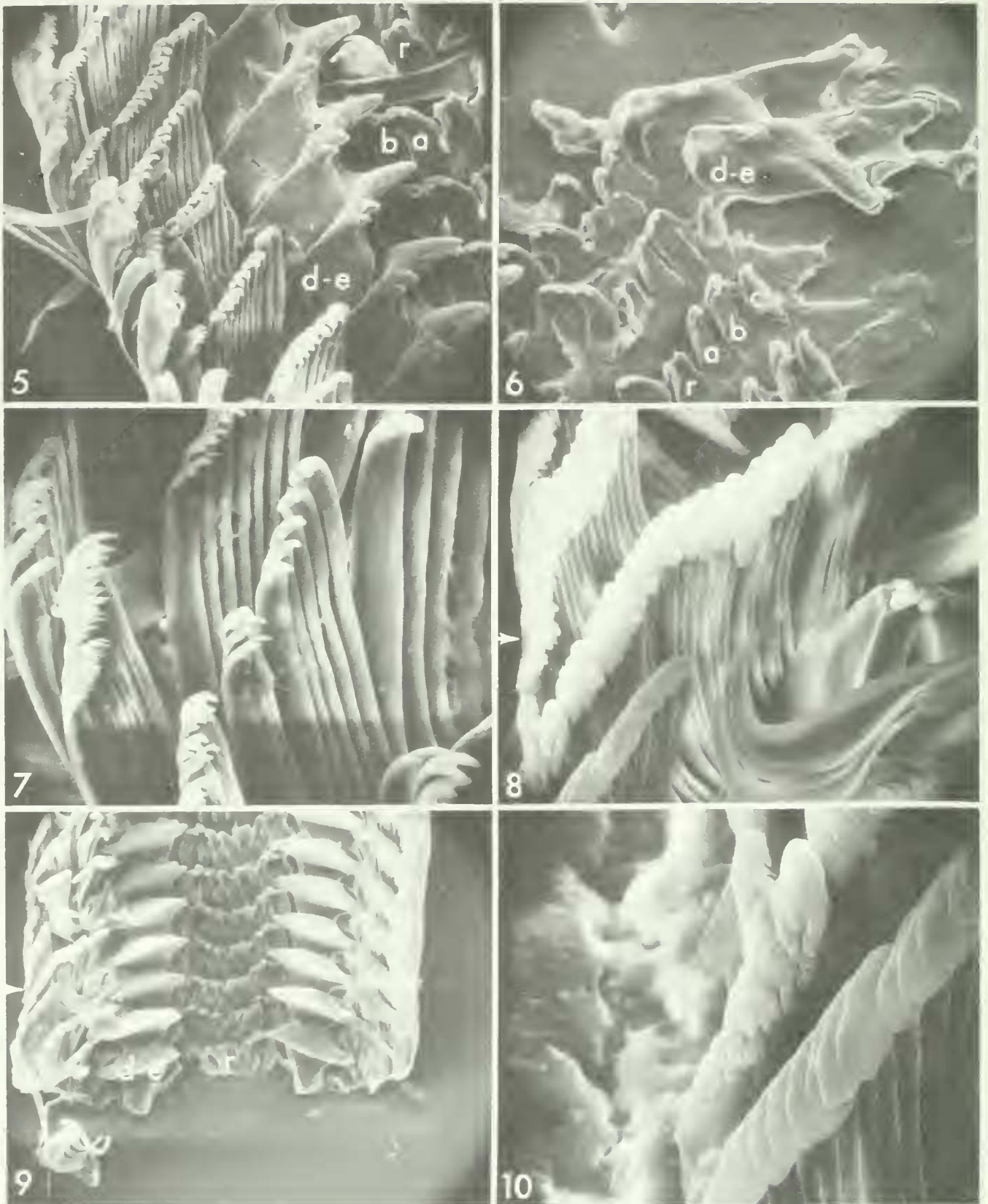
rests. Respiration facilitated by open mantle cavity which effectively forms a lung. Mantle unpigmented except for a few diffuse patches of gray over the pallial genitalia and lower half of hypobranchial gland. A very short columellar cleft extends posteriorly to point just behind mantle collar (Fig. 4). Right columellar retractor muscle broad, triangular, and attached to shell at posterior end of cleft. Left columellar retractor similar but about half as large. Roof of mantle cavity heavily supplied with large transversely alternating arteries and veins. Blood vessels most abundant posteriorly and in mid-region, sparse and smaller just behind mantle collar. Genitalia and rectum terminate just behind mantle collar.

Hypobranchial gland (Figs. 4, 12) very large, extending along dorsal (right) side of mantle wall from posterior edge of renal cavity to about middle of pallial genitalia. Hypobranchial duct (Fig. 12) lying between columellar angle of mantle cavity and lower genitalia, open along anterior mesad half which is densely lined internally with large conical papillae.

**Pallial complex:** Pericardium a large sac



FIGS. 1-4. Soft anatomy of *Proserpina* and *Ceres*. Fig. 1. *Proserpina nitida* Sby.—ventral view of pallial organs. Fig. 2. *P. nitida*—dorsal view of female with shell removed. Fig. 3. *Ceres nelsoni* Dall—inner view of pallial organs. Fig. 4. *C. nelsoni*—dorsal view of female with shell removed. Scales in mm.



FIGS. 5-10. Scanning electron micrographs of radulae of *Ceres nelsoni* Dall (Figs. 5-7) and *Proserpina nitida* Sby. (Figs. 8-10). Fig. 5.  $\times 339$ . Fig. 6.  $\times 133$ . Fig. 7.  $\times 324$ . Fig. 8.  $\times 632$ . Fig. 9.  $\times 316$ . Fig. 10.  $\times 1270$ . Fig. 8 is an enlargement from area of arrow in Fig. 9. Fig. 10 is an enlargement from area indicated by arrow in Fig. 8. Symbols: r—rhachidian tooth; a, b, c—A-lateral, B-lateral, C-lateral; d-e—capituliform complex (D-plate & E-plate).

just under ventral side of mantle at columellar angle, overlapping anterior half of kidney and part of loop of intestine, and communicating with renal cavity through small renal-pericardial pore lying at base of renal papilla and apex of left auricle. Heart consisting of ventricle and two auricles (Fig. 3); left auricle underlying kidney and receiving efferent pulmonary vein from roof of lung. Right auricle smaller than left, posterior to ventricle and receiving two veins; one from anterior viscera and one from posterior gonadal viscera.

Kidney (Fig. 3) broadly bean-shaped and lying along ventral surface of intestine and partially dorsal to left auricle. Renal papilla clearly distinguishable only near anterior end of kidney, terminating as short ovoid papilla discharging into posterior end of mantle cavity.

*Radula* (Figs. 5–7, 11): Central field consisting of rhachidian tooth and five lateral teeth. Rhachidian tooth simple, trapezoidal, with broad blunt edge (Fig. 6). Basal ligament thin and membranous, lower margin not clearly defined as are basal ligaments of A-, B-, and C-laterals. A-lateral with weak reflection bearing 3 large acuminate cusps, center one

slightly larger. B-lateral with single broad, bluntly pointed central cusp and short blunt cusp on each side. C-lateral with single broad cusp. Capitulum complex consisting of two separate interlocked teeth, the D-lateral and the E-lateral, otherwise referred to as the comb-lateral (D) and the accessory plate (E). Comb lateral (Figs. 5, 11) as in Helicinidae, bearing enlarged acuminate cusps along its rasping edge. Innermost cusp largest, followed laterally by two or three smaller, nearly equal-sized cusps. Outer edge of comb-lateral interlocking into mesad edge of accessory plate to form capitulum complex, a structure superficially appearing as single tooth. Outer edge of radula containing about 45 marginal teeth on each side (Fig. 7). Marginals with expanded bases that attach to basal membrane. First eight marginals bicuspid (Fig. 11); cusps large and rounded; marginals 9–16 tricuspid; outermost marginals with 5 cusps each. I was unable to determine transition point from 4 to 5 cusps because of torn condition of radula examined.

*Female reproductive system* (Figs. 12, 13): Ovary unpigmented, large and discoidal, lying over anterior (cephalic) half of digestive

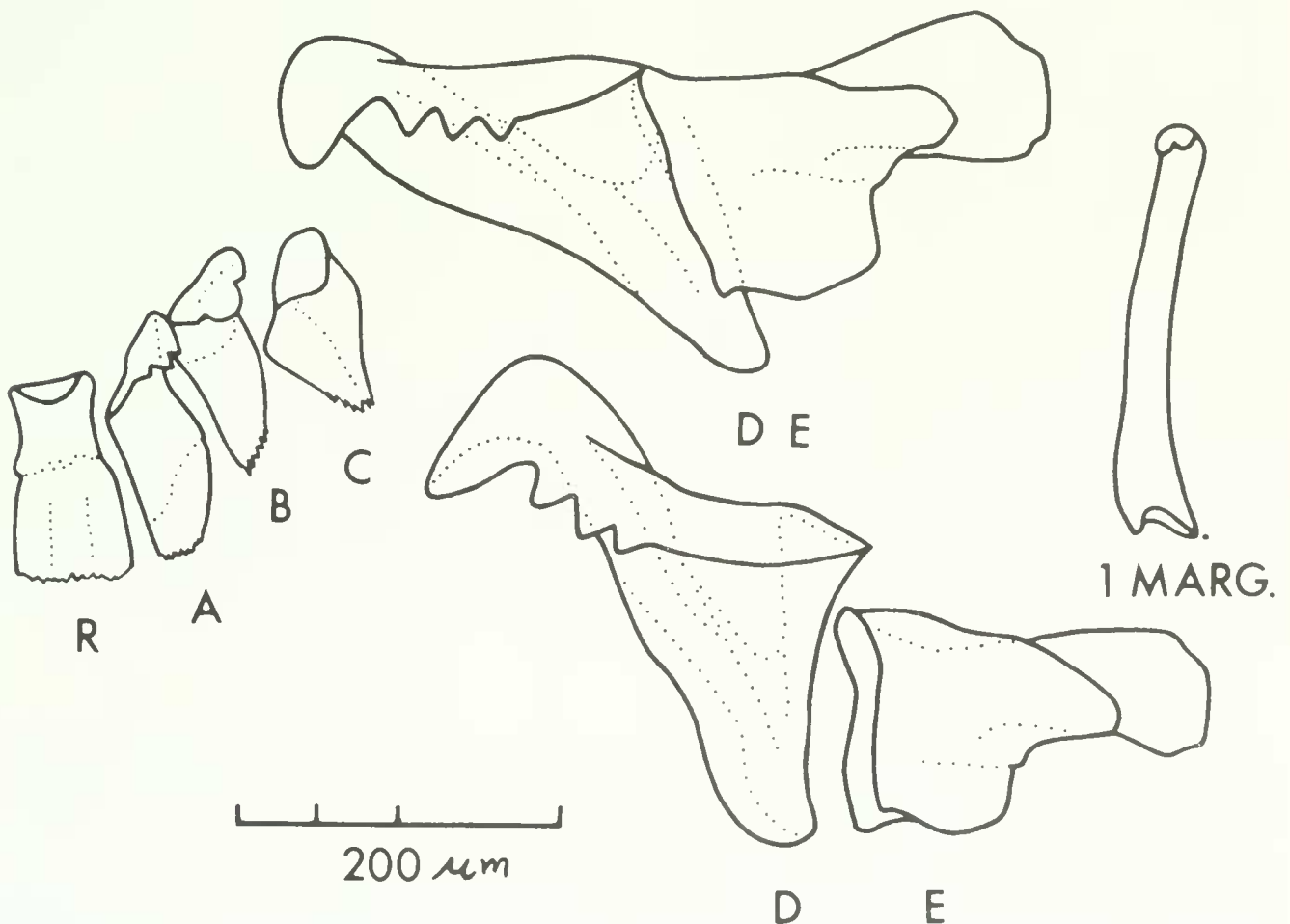


FIG. 11. Radula of *Ceres nelsoni* Dall. R—rhachidian tooth; A, B, C-lateral teeth; D, E-lateral field forming capitulum complex.

gland, and folding partially beneath; consisting of numerous small lobules discharging into collective tubules leading into ovoid egg sac at mesad side of ovary. Primary oviduct short, thick. Pallial genital system (secondary oviduct and associated organs) with two female openings: vaginal opening receives sperm, oviducal opening passes fertilized eggs. Vaginal opening at posterior right corner of mantle cavity just anterior to primary oviduct, and ventral to hypobranchial duct, *not* inside hypobranchial duct as in Helicinidae. Vaginal complex (Fig. 13) consists of short papilliform vagina leading into seminal receptacle and bearing on its upper side large, elongate, weakly lobed provaginal sac and smaller ovoid bursa copulatrix. Provaginal sac wrapped over dorsal side of seminal receptacle and bursa copulatrix, lying on ventral side of V-organ when in natural position (Fig. 12).

Posterior end of secondary oviduct beginning with ascending limb of V-organ, which together with accessory sperm sac form a T-shaped structure on top of descending limb (pedicel). Accessory sperm sac a single large bulb, lying on left side of apex of pedicel and about as large as ascending limb. Pedicel short and stocky, entering into thin-walled seminal receptacle continuing anteriorly into uterus. Uterus strongly folded externally but without accessory ducts or diverticula. Crystalline gland absent at base of uterus. Oviducal opening and anus separate but adjacent just behind mantle collar.

*Male reproductive system* (Fig. 14): Testis similar to ovary in shape and position but with considerably larger lobes. Like ovary, testis partially folded around anterior edge of digestive gland. Vas deferens short and thick, entering apex of prostate at oblique angle. Apex of prostate forming short elliptical chamber continuous with lower chamber of prostate, and occupying same position as provagina in male *Proserpina* and Helicinidae, but histologically not different from prostate. Ventral surface of prostate strongly folded with transverse wrinkles; dorsal surface with elongate field of glandular folds and tubules. Prostate not clearly demarcated into upper and lower segments as in *Proserpina* and the Helicinidae. Elongate field of glandular folds along posterior extremity corresponding to limit of prostate-I in helicinids. Lower prostate very short and otherwise not demarcated. Base of prostate forming short voluminous terminal chamber and bearing two short caeca just above male opening. One caecum overlaps

the other, so only a single one evident superficially. Posterior edge of terminal chamber giving rise to long stout diverticulum appressed against ventral side of prostate and extending to posterior end of prostate-I. Diverticulum regularly creased externally into transverse segments throughout its length and having long longitudinal internal folds partially dividing lumen into parallel chambers. Diverticulum bearing near its base a short stout appendix. Terminal chamber of prostate and intestine having a common opening.

#### *Ceres salleana* Gray

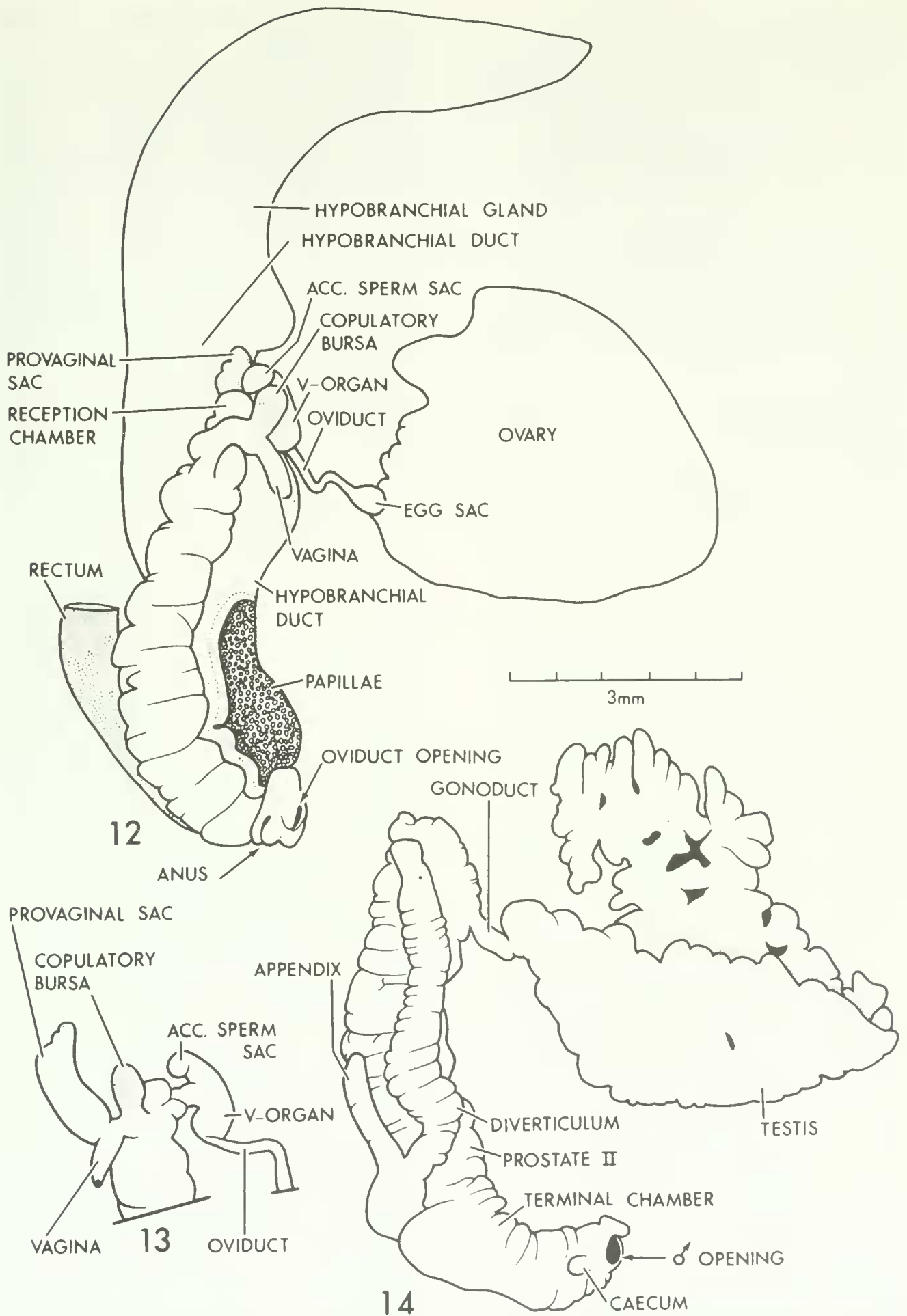
Gray (1856) gave observations on external morphology of the animal and described and illustrated the radula. Boss & Jacobson (1975a: 61) rejected Gray's data on the basis that they suspected Gray had confused the radula of a *Helicina* for *C. salleana*. In light of the information on the radula of *C. nelsoni*, Gray's data must be accepted.

Gray's description and illustration of the radula of *C. salleana* do not properly depict the structure of the capituliform complex. Aside from this difficulty he demonstrated that the radula of *C. salleana* is like that of *C. nelsoni*. Following is a quote of his description:

"... the central rhachidian tooth is oblong, with a smooth, recurved tip, the 1st and 2nd internal teeth A- and B-laterals rather broader than the central, with a three-toothed recurved tip, the 3rd C-lateral narrow, elongate, with a slight recurved end, the 4th and 5th D- and E-laterals, the capituliform complex much larger, oblong and irregular in shape, the 4th about half the width of the 5th, with 3 or 4 denticles on the inner side of the upper edge; the 5th very large, broad, with a large sub-central reflexed lobe; the lateral marginal teeth are very numerous, subequal, compressed, transparent, with a recurved tip, which in the inner teeth of the series is bifid."

#### *Linidiella swifti* (Bland)

Thiele (1931: 90) gave a brief description and figure of the radula of *L. swifti*, which is redrawn (Fig. 24) from his figure. Boss & Jacobson (1975a, b) in their review of the proserpinids overlooked this description. Thiele only briefly described and illustrated the central field, consisting of the rhachidian tooth, the A-, B-, and C-laterals, and the



FIGS. 12-14. Reproductive system of *Ceres nelsoni* Dall. Fig. 12. Female system. Fig. 13. Posterior segment of female system with oviduct and associated structures partially separated to show interrelationships of organs. Fig. 14. Male system.

capituliform complex. These teeth are basically similar to those of *Ceres*. The A-, B-, and C-laterals bear about 3 weak cusps along the cutting edge. The D-plate of the capituliform complex is a comb-lateral with about seven distinct acuminate cusps. The innermost cusp is the largest, and the following cusps decrease in size progressively.

*Proserpina (Proserpina) nitida* Sowerby

The following anatomical data are based upon a large series of preserved specimens collected by Glenn Goodfriend 1.3 mi S. Clarmont, St. Ann Parish, Jamaica, 1 November 1976.

*External anatomy:* Foot (Fig. 2) long, slender, keeled above; sole undivided longitudinally; aulacopod, bordered on each side by double row of crenulations. Caudal pore absent, sides lightly spotted with melanophores. Snout white, relatively elongate, separated from foot by deep groove. Pedal gland groove extending around anterior edge of foot and continuing posteriorly with aulacopod groove. Tentacles long, slender, dark gray with light stripe on posterior surface. Eyes at outer base of tentacles. Mantle lappet spotted and mottled like foot but more intensely, nearly uniformly wide, extending posteriorly over edge of shell, and complete around body. Lappet widening over posterior foot and forming pad supporting shell.

Both right and left columellar retractors extend into shell for about one whorl. Both bands slender and dilated near their attachments to shell. Columellar cleft extending posteriorly for about  $\frac{3}{4}$  whorl, separating lower body from upper viscera.

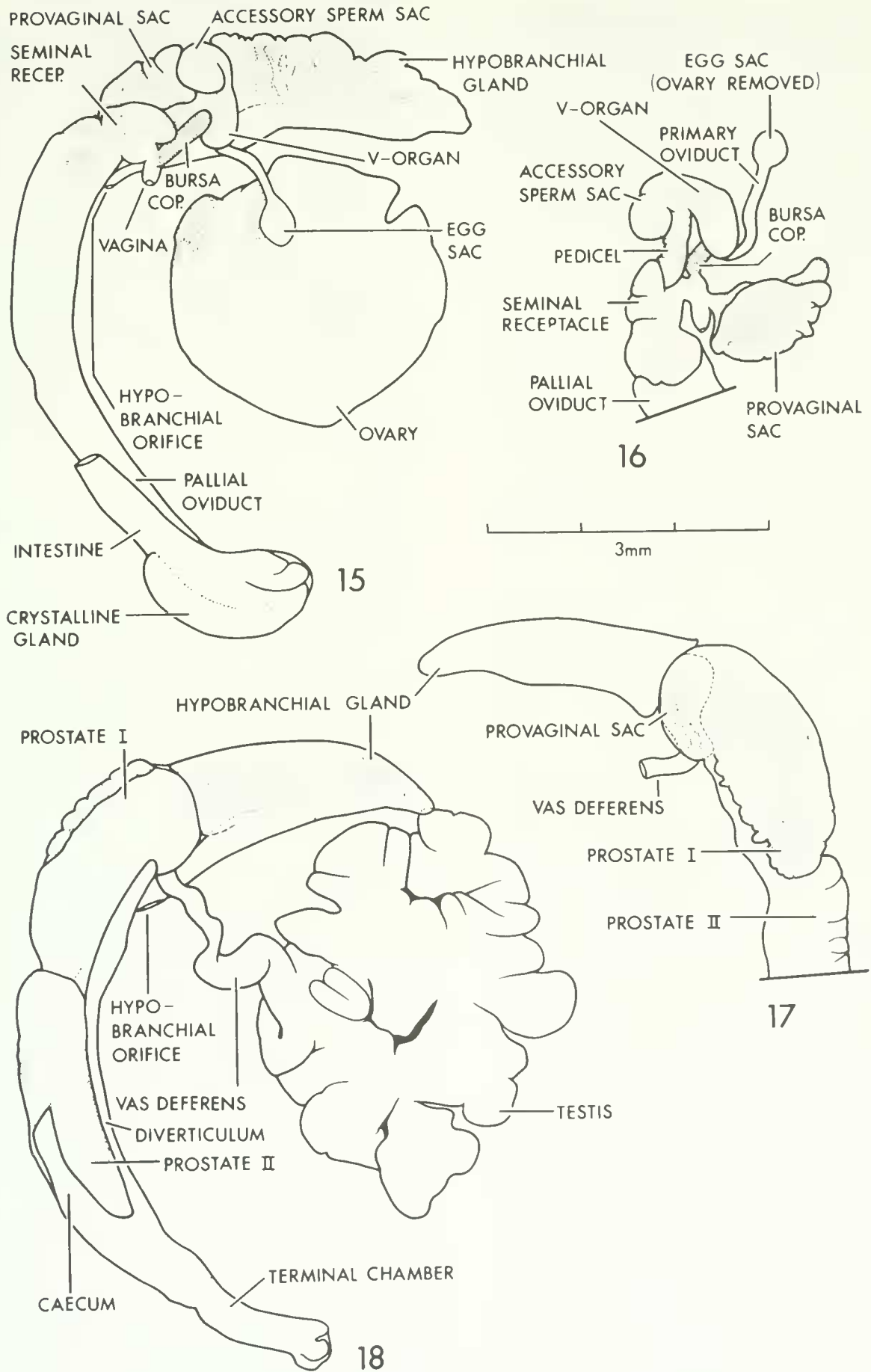
*Pallial organs:* Mantle unpigmented, except over liver and gonad where it is dark gray. Internal organs easily viewed through mantle. Intestine and lower reproductive system terminate about  $\frac{1}{4}$  whorl behind mantle collar. Outer lung wall with very sparse network of small veins most concentrated behind collar (pallial organs shown from ventral surface with mantle removed, Fig. 2). Kidney narrowly concentric, forming a semicircular arch just behind pericardium and beneath loop of intestine. Renal papilla a low ridge on anterior end of kidney, short, blunt and protruding into posterior end of mantle cavity. Pericardium lying beneath left end of kidney but extending obliquely over right end. Right auricle absent. Ventricle slightly wider but shorter than left auricle, receiving anteriorly efferent pulmo-

nary vein, and along left edge two smaller veins from viscera.

*Radula* (Figs. 8–10): Radula not remarkably different from that of *P. depressa* as described by Baker (1926b). Rhachidian tooth simple, parallel-sided and lacking reflection. A-, B-, and C-laterals each with single cusp (radula illustrated, Fig. 9, has anomalous duplicate A-lateral on left side). As in *P. depressa*, A-lateral smaller than B-lateral. Capituliform complex with very heavy scraping cusp on D-plate. Marginal field consisting of 43 blade-like teeth; first 27 unicuspid with sharp anterior edge (Fig. 9); next six bicuspid; next eight (Fig. 10) tricuspid; outermost two with 4–5 long weak cusps each. Inner marginals consisting of broadly triangular plates thickened at base, twisted posteriad, and reflected at upper angle to form spatulate blades. Marginal teeth increasing in length laterally through about 28th tooth; then becoming shorter and narrower at base.

*Female reproductive system* (Figs. 15–16): Ovary very large and circular, occupying almost entire dorsal surface of digestive gland, consisting of multitude of small, convoluted, compactly coiled lobes which discharge into small converging ducts that lead into a relatively large oval egg sac on base of ovary. Primary oviduct short, thick, extending from egg sac to pallial oviduct where it enters through short limb of V-organ. Hypobranchial gland completely posterior to pallial oviduct, discharging into mantle cavity by a short duct. Pallial oviduct bearing at distal end two bulbous structures on end of relatively long pedicel; short, cylindrical V-organ on right side of pedicel, and a large bulbous accessory sperm sac on left side. Sperm sac analogous, not homologous, to accessory sperm sac in Helicinidae. In latter group accessory sperm sac located at end of short duct on side of pedicel; no such structure present in *P. nitida*. V-organ and accessory sperm sac entering a relatively long pedicel that discharges into posterior end of seminal receptacle (Fig. 16). Vagina a short bulbous structure protruding into posterior angle of mantle cavity along left side of pallial oviduct posterior to hypobranchial opening; bearing large weakly lobed provagina and small bursa copulatrix. Provagina wrapped around dorsal side of reception chamber and pedicel; bursa copulatrix lying on ventral side and extending posteriorly. These structures are unwrapped from vagina (Fig. 16) to show interrelationships. Seminal receptacle entering long slen-





FIGS. 15-18. Reproductive system of *Proserpina nitida* Sby. Fig. 15. Female reproductive system. Fig. 16. Posterior segment of female system with oviduct and associated structures partially separated to show interrelationships of organs. Fig. 17. Male reproductive system. Fig. 18. Ventral view of prostate showing vestigial provaginal sac.

der pallial oviduct-II, bearing at its anterior end elongate crystalline gland. Oviduct and anus close but separate.

*Male reproductive system* (Figs. 17–18): Testis, like ovary, a large circular mass imbedded on dorsal side of digestive gland; consists of numerous lobes similar to, but much larger than those forming ovary. Vas deferens short and stout, entering end of provagina, which is embedded in posterior end of prostate-I (Fig. 18). Prostate-I strongly folded dorsally and continuing into longer, more slender prostate-II, which bears a long, clearly demarcated terminal chamber. Diverticulum originating at junction of prostate-II and terminal chamber, lying along ventral surface of prostate and extending posteriorly to point where vas deferens enters provagina; diverticulum with short, broad appendix about a third of the length of prostate-II. As in female, hypobranchial gland in male lying completely posterior to pallial gonoduct and discharging into mantle cavity by short duct.

*Proserpina (Despoenella) depressa* (Orbigny)

Baker's (1926b) description of the radula is quoted here for comparison with *P. (s.s.) nitida* Sowerby:

"The rhachidian central . . . consists of a thin plate with parallel sides. Its anterior edge is weakly notched and has no sign of a reflection or cusp, although its anterior half is slightly thickened. Its posterior edge is very thin, quite irregular and somewhat pointed. The A-central (A) is smaller than the B-plate (B) which is the reverse of their relative sizes in the Vianinae. . ."

"The D-plate is a T-lateral with a broadly crescentic reflection (about half as deep as wide) and a short, stout, stalk. Under dry lenses its cutting edge appears simple and smooth, but under an oil-immersion objective, the entire upper surface is seen to be beautifully striate at right angles to its free margin, which as a result becomes very minutely serrate in worn teeth. The E-plate (E) is relatively larger than, but quite similar in structure to that of most Vianinae; its upper one-fourth is very firmly cemented behind the outer portion of the D-lateral."

". . . fifty-three to fifty-five uncini are present on each side. The first twenty-two are unicuspid; the next three to five are bicuspid; while the outer teeth increase the number of cusps. The innermost marginals consist of a broadly triangular plate which is thickened at the base and twisted posteriorly and reflected at its upper angle so as to form a spatulate blade. The teeth increase in length from the

inside out and the blades become larger out to about the 12th tooth. The outer marginals are lingulate and multicuspid; the outermost (40, 55) have broad reflected tips with numerous cusplets . . . another specimen has 66 marginals on each side."

## MAJOR TAXA AND PHYLOGENY

### Superfamily relationships

Current classifications of the Gastropoda generally recognize three subclasses: Prosobranchia, Opisthobranchia, and Pulmonata. The Prosobranchia in turn are divided into three orders: Archaeogastropoda, Mesogastropoda, and Neogastropoda (Keen, 1960; Fretter & Graham, 1962; Taylor & Sohl, 1962).

Golikov & Starobogatov (1975) divided the Prosobranchia into three subclasses equal in rank to the Opisthobranchia and Pulmonata: Cyclobranchia, Scutibranchia, and Pectinibranchia. They placed the Turbinomorpha and the Neritimorpha in the Pectinibranchia along with most other prosobranchs otherwise referred to as the Mesogastropoda and Neogastropoda. However, the Turbinomorpha and the Neritimorpha are more like the Scutibranchia in most of their anatomical traits and do not conform to their definition of the Pectinibranchia. For this reason, in part, the earlier classification of the Prosobranchia into Archaeogastropoda, Mesogastropoda, and Neogastropoda is followed in this paper.

The Archaeogastropoda are also referred to as the Diotocardia because of the presence of two auricles on the heart. The Mesogastropoda and the Neogastropoda are collectively referred to as the Monotocardia because of the presence of a single auricle. The Diotocardia have, in general, paired gills, two kidneys, two columellar retractor muscles, and the anal and genital openings at the posterior end of the mantle cavity. Wastes and reproductive products are liberated into the mantle cavity whence they are conveyed to the outside by excurrent water currents.

With the evolution of a conspiral shell there is a strong trend toward reduction of paired organs to single organs because of mechanical pressure on the right side of the pallial region due to allometric growth of the left side. Coupled with this allometric growth is a change in the flow of water current into and out of the mantle cavity, so that the location of a gill on the left (incurrent) side and the loca-

tion of excretory openings on the right (excurrent) side are favored. These trends culminate in the Monotocardia with the evolution of a single (left) auricle, a single (left) gill, a single (left) kidney, a single (right) retractor muscle, a pallial gonoduct that conveys reproductive products to the anterior right corner of the mantle cavity, and an extension of rectum to the anterior right corner of the mantle cavity.

The mollusks constituting the subject of the paper belong to the Superfamily Helicinacea, which in turn belongs to the Infraorder Neritimorpha. The Neritimorpha is an infraorder within the Archaeogastropoda. The Helicinacea are defined as follows:

#### HELICINACEA Thompson, *new superfamily*

Primitive pulmonate archaeogastropods with an exogastric septate shell. Primitively non-operculate. Primitive members with a lamellar barrier partially blocking aperture. More advanced members secondarily operculate. Lung a vascularized open mantle cavity. Gill and osphradium absent. Reproductive system diallic or triaulic, with two or three functional openings. Pallial gonoduct well developed. Spermatophores absent. Pallial rectum present, conveying waste products to outside of mantle cavity. Hypobranchial gland discharging into mantle cavity via a duct, incorporated into reproductive system in the Helicinidae. Pedal nerve cords nearly parallel, and bearing primitive lattice-like arrangement of connectives; supra-intestinal nerve absent; zygoneury occurring between pleural ganglia, and almost occurring between pleural and pedal ganglia and between pedal-pedal ganglia, which are only demarcated by narrow zones where connectives would normally be. Radula rhipidoglossate with central field consisting of single rhachidian tooth. Lateral field consisting of A-, B-, and C-lateral, and next two teeth (rasping or scraping teeth), that combine to form capituliform complex in which D-lateral is functional rasping or scraping tooth.

Within the Neritimorpha the Helicinacea appear to be most closely related to the Neritacea (Neritidae and Septariidae) on the basis of similar radulae, diallic reproductive systems, and nervous systems. The Family Hydrocenidae frequently is placed in close relationship with the Helicinidae, but the hydrocenid radula, monaulic reproductive system, and single (right) columellar retractor

muscle are so divergent from the more primitive anatomical states of the Helicinacea that only a remote relationship can be established on the basis of morphological data (Thiele, 1910; Bourne, 1911; Baker, 1925). The Hydrocenidae should be placed in a separate superfamily, the Hydrocenacea Troschel, 1856, within the Neritimorpha.

The Helicinacea generally have been considered the most advanced group of the Archaeogastropoda because the only information available on the anatomy of the superfamily relates to various species of Helicinidae, the most specialized of the three families in the Helicinacea (Isenkrahe, 1867; Bourne, 1911; Baker, 1925, 1926a, 1926b; Thiele, 1931; Boss & Jacobson, 1975a). The various anatomical traits were attributed, in part, to the evolution of a conspiral shell. Characters in the Helicinidae supporting that classification are: (1) the absence of a right kidney, (2) the presence of a complete pallial gonoduct, (3) the presence of a rectum extending to the front of the mantle cavity, (4) the absence of a right auricle and, (5) the absence of gills. Within the Archaeogastropoda traits (2) and (3) occur only in the Neritimorpha but they are present in nearly all Mesogastropoda and Neogastropoda. These traits are not necessarily advanced morphological traits consequential of the development of a conspiral shell as has been suggested. An alternative hypothesis is that they are consequences of the evolution of a *land snail* from a diotocardian *marine ancestry*. To begin with, neither the Helicinacea nor the Neritacea has a conspiral shell. Basically the shell is limpet-like. Growth occurs in an exogastric direction with partial distortion to the right; but as the shell grows, the right wall dissolves away internally and produces a septate shell. The extent to which growth occurs is evident externally by the number of volutions produced on the apex; internally the only change that has occurred is an increase in space. The snail's body remains limpet-like. In this respect the shell and body of the Helicinacea and the Neritacea are more primitive than the shell and body of the Turbinimorpha which are truly conspiral.

Early in the evolution of the Gastropoda the primary gonoduct evolved to empty into the right renal duct, thus incorporating the right kidney into the reproductive system. Adaptation to a terrestrial environment requires an albumen coating for the egg which serves as a protective aqueous environment in which

the developing embryo can transform without danger of desiccation. This adaptation was accomplished by the evolution of the right kidney into the albumen-secreting provaginal sac of the Helicinacea (Baker, 1925), the precursor of the albumen gland of the Neritacea and higher gastropods. In addition, the evolution of a pallial gonoduct is prerequisite to a terrestrial mode of existence. Archaeogastropods, other than the Neritimorpha, have a simplified reproductive system in which eggs and sperm are released at the posterior end of the mantle cavity and are conveyed by water currents to the outside where fertilization takes place. A terrestrial mode of existence requires the evolution of structural devices to facilitate fertilization and ovipositing to replace the water transport mechanisms of more primitive forms. Thus the pallial gonoduct of the Helicinacea is an adaptation for a terrestrial existence. This adaptation would be required for any terrestrial mollusk regardless of its phylogenetic level, and does not necessarily reflect a higher phyletic level.

Coupled with the evolution of a pallial gonoduct is the evolution of a rectum that conveys waste products outside the mantle cavity. Archaeogastropods, other than the Neritimorpha, are not confronted with the problem of fouling of the mantle cavity for they are aquatic and the mantle cavity is continually flushed by water currents. However, a terrestrial snail does not have this cleansing mechanism and the evolution of a pallial rectum is a necessary adaptation to prevent fouling of the mantle cavity. As a matter of fact, there would be far greater adaptive pressure to evolve a pallial rectum in terrestrial gastropods than in aquatic groups.

Loss of the right auricle of the heart has occurred in most species of the Helicinacea, although two auricles still persist in the two most primitive groups within the superfamily. In *Ceres* (Ceresidae) the right auricle is functional and is nearly as large as the left. In *Hendersonia* (Helicinidae, Hendersoniinae) the right auricle is functional but very much reduced in size. In other helicinaceans the right auricle is lost. The loss of the right auricle in more advanced neritimorphs is a consequence of the crowding of the right side of the pallial region by the pallial gonoduct.

Clearly the loss of a gill is an adaptation for a terrestrial existence, and its absence in the Helicinacea is to be expected. In this connection it should be noted that the gill of some neritids may not be homologous to the gill of

other neritaceans. Fretter & Graham (1962: 307) and Bourne (1908: 853) show that in *Theodoxus*, a freshwater neritid, the gill is innervated by the left pleural ganglion, rather than the supraoesophageal ganglion as occurs in other archaeogastropods. It may be argued that the gill of *Theodoxus* is a new structure evolved to accommodate an aquatic existence in a snail that evolved from a gill-less ancestor. This view was favored by Simroth (1896–1907, 1910) and von Ihering (1877). The only difference between the nervous system of Neritacea and that of Helicinacea is in the divergence of the pedal nerve cords. In the Neritacea the cords strongly diverge at about a 60–75° angle (Bourne, 1908), which probably is a modification consequential to the widening of the foot for adhesion to the rock substrate of an aquatic environment by a limpet-like snail. In Helicinacea the pedal cords are nearly parallel (Bourne, 1911; Baker, 1925; this study, *Ceres nelsoni*, *Proserpina nitida*), which correlates with the narrow, more mobile foot required for terrestrial movement.

The nervous system of Helicinacea, like Neritacea, shows a specialization through zygoneury and loss that make it unlikely that either group could have been ancestral to other orders of Prosobranchia or to the Pulmonata.

From the foregoing data, it is apparent that the Helicinacea are a gill-less pulmonate assemblage of land snails that are properly placed in the Diotocardia. This group has a simplified arrangement of pallial organs due to a reduction in the number of heart chambers and excretory organs and the loss of a gill and an osphradium. A pallial gonoduct and rectum were evolved to accommodate terrestrial existence, and the hypobranchial gland is modified to discharge into the mantle cavity through a duct. Primitively this group was non-operculate, protecting the opening of the limpet-like shell with a partial septum and a lamellar barrier (Ceresidae, Proserpinidae). Secondarily, an operculum was evolved to close the aperture (Helicinidae). Which group of marine mollusks was ancestral to the Helicinacea is not clear. However, it is apparent that on the basis of the shell, the operculum, the gill, the radula (Baker, 1923b), the heart, and the reproductive system (Fretter & Graham, 1962; Bourne, 1908) the Neritacea is not ancestral to the Helicinacea. Internal fertilization through a pallial gonoduct and the complete pallial rectum of the Helicinacea of-

fer advantages that allow these systems to persist in more advanced aquatic groups. They are not required for an aquatic mode of life (as in the Turbinimorpha), but they are required for a terrestrial mode of life. Once evolved they are likely to be retained in terrestrial or aquatic lineages.

#### FAMILY RELATIONSHIPS WITHIN THE HELICINACEA

The Helicinacea include three families, the Helicinidae, Ceresidae, and Proserpinidae. The Helicinidae is further divided into three subfamilies, Helicininae, Hendersoniinae and Vianinae. The latter two subfamilies apparently are natural groups definable by anatomical criteria and shell characteristics. The Helicininae are a heterogeneous assemblage that includes several disparate groups. Two of these ("Ceratomiscinae" and "Stoastomatidae") are separable from the helicinids (s.s.) on the basis of shell and opercular traits. The few observations published on their radula do not show significant differences from Helicininae (Pilsbry & Brown, 1910; Baker, 1922; Thiele, 1927). All other aspects of stoastomid and ceratomiscid soft anatomy are unknown, and so they are excluded from further discussion in this paper (see Boss, 1972, for a discussion of the subgenera of *Stoastoma* and Boss, 1973, for a monograph of *Ceratomiscus*).

Twenty-three characters are useful for separating families and subfamilies within the Helicinacea and for showing relationships among the groups involved. Because of the structural diversity that occurs within the Helicinidae, it is necessary to redefine the family and its two subfamilies Hendersoniinae and Vianinae in order to discuss relationships within the Helicinacea.

#### CERESIDAE Thompson, *new family*\*

*Type-genus: Ceres* Gray, 1856.

This family has the following combination of characteristics: SHELL: (1) operculum absent; (2) periostracum present; (3) shell marked with radial sculpture. EXTERNAL ANATOMY: (4) foot holopod; (5) mantle collar not extending out over shell; (6) tentacles long, slender; (7) axial cleft separating last whorl very short, about 0.1 whorl long; (8) heart with two functional, nearly equal-sized

auricles; (9) kidney broad, irregularly ovate in shape; (10) hypobranchial gland very long, overlapping posterior half of pallial gonoduct; (11) hypobranchial duct extending length of pallial oviduct; open along lower half. REPRODUCTIVE SYSTEM: (12) rectum and pallial gonoduct terminating at mantle collar; (13) vagina opening directly into posterior corner of mantle cavity, not inside hypobranchial duct; (14) gonad large, flattened, oval in shape; (15) egg sac present at origin of primary oviduct; (16) primary gonoduct very short, thick; (17) prostate not divided into upper and lower division, provaginal sac absent in males; (18) accessory sperm sac consisting of tubular bulb at left end of pedicel opposite ascending limb of V-organ; (19) crystalline gland absent. RADULA: (20) A-, B-, and C-lateral teeth with 2-3 serrated cusps; (21) capituliform complex consisting of a comb-lateral (D-lateral) and accessory plate (E-lateral); (22) accessory plate (E-lateral) with broad wing enveloping end of D-lateral; (23) innermost marginal teeth with three cusps, outer marginals polycuspid.

Characteristics 7, 8, 9, 10, 11, and 17 are unique to the Ceresidae.

A prior family-group taxon name, Proserpinellinae (Baker, 1923a) was proposed for members of this family, based upon the oldest named genus within the group. Considering the scant information available about *Proserpinella* it is ill-advised to base a family name on a genus that is so poorly known. There is no marked precedent in malacology for giving priority to the oldest name available for families (Baker, 1956a, 1956b), nor can there be where so many names were spuriously founded.

#### Family PROSERPINIDAE Gray, 1847, REDEFINED

*Type-genus: Proserpina* Sowerby, 1839.

SHELL: (1) operculum absent; (2) periostracum absent; (3) shell smooth, without radial or spiral sculpture. EXTERNAL ANATOMY: (4) foot aulacopod; (5) mantle collar extending fully or partially out over shell; (6) tentacles long and slender; (7) axial cleft about  $\frac{3}{4}$  whorl long; (8) heart with single auricle (left); (9) kidney narrowly crescent-shaped; (10) hypobranchial gland short, triangular in shape, confined posteriorly to pallial gonoduct; (11) hypobranchial duct short, opening at posterior

\*Thompson has already used this name in an abstract (*Bulletin of the American Malacological Union* for 1979 [published early 1980], p. 63). EDS.

end of mantle cavity. REPRODUCTIVE SYSTEM: (12) rectum and pallial gonoduct terminating some distance from mantle collar as in Hendersoniinae; (13) vagina opening directly into posterior mantle cavity, not into hypobranchial duct; (14) gonad huge, discoidal; (15) egg sac present at origin of primary oviduct; (16) primary gonoduct very short, stout; (17) prostate divided into two divisions, prostate-I and prostate-II; provaginal sac vestigial within prostate-I; (18) accessory sperm sac consisting of tubular bulb at left end of pedicel opposite ascending limb of V-organ; (19) crystalline gland present at base of pallial oviduct. RADULA: (20) A-, B-, and C-lateral teeth unicuspid; (21) capituliform complex consisting of T-lateral (D-lateral) and accessory plate (E-lateral); (22) accessory plate (E-lateral) reduced in size, without wing; (23) innermost marginal teeth unicuspid. Outer marginals with few to several cusps.

Characteristics 2, 3, 4, 5, 10, 17, and 19 are unique to the Proserpinidae.

Family HELICINIDAE (HELICININAE)  
Férussac, 1822, REDEFINED

*Type-genus: Helicina* Lamarck, 1799.

(For anatomical data see Thiele, 1902; Bourne, 1911; Baker, 1926a.)

SHELL: (1) operculum present, concentric; (2) periostracum present; (3) shell marked with radial and/or spiral sculpture. EXTERNAL ANATOMY: (4) Foot holopod; (5) mantle collar not extending out over edge of shell; (6) tentacles long and slender; (7) axial cleft separating last whorl of body about  $\frac{1}{2}$  whorl long; (8) heart with single auricle (left); (9) kidney narrowly concentric in shape; (10) hypobranchial gland elongate, overlapping posterior end of pallial gonoduct; (11) hypobranchial duct not extending beyond posterior half of pallial gonoduct. REPRODUCTIVE SYSTEM: (12) Rectum and pallial gonoduct terminating just behind mantle collar; (13) vagina opening into hypobranchial duct (female diaulic); (14) gonad smaller, elongate; (15) egg sac absent on primary ovary; (16) primary gonoduct relatively long; (17) prostate divided into prostate-I and prostate-II. Provaginal sac absent in males; (18) accessory sperm sac located near middle of right side of pedicel, consisting of small bulbous sac at end of short narrow duct; (19) crystalline gland absent. RADULA: (20) A-, B-, and C-laterals usually with several cusps; cusps frequently reduced or absent on

A-lateral; (21) capituliform complex consisting of comb-lateral (D-lateral) and accessory plate (E-lateral); (22) accessory plate with or without wing enveloping end of D-lateral; (23) innermost marginal teeth with 2–3 cusps. Outer marginals polycuspid.

Only four traits found in all species examined are unique to the Helicinidae (s.l.) This small number is due to the anatomical diversity within the family and the structural modifications and losses that have occurred within the various phyletic lines. These traits are: (1) operculate, (13) vagina opening into hypobranchial duct, (14) gonad small and elongate, and (16) primary gonoduct moderately long.

Within the Helicinidae several trends occur which progress from generalized states, as found in the Hendersoniinae, to modified states, as found in the Helicininae on the one hand and in the Vianinae on the other (Baker 1925, 1926a). These include: (a) modification of operculum from paucispiral type to concentric type, (b) increasing complexity of shell sculpture, (c) reduction and loss of right auricle, (d) increased length of pallial gonoduct and hypobranchial duct, (e) simplification and elongation of female primary oviduct, (f) translocation of accessory sperm sacs on pedicel, (g) general reduction of cusps on radular teeth, (h) tendency for D-lateral tooth to change from comb-lateral to T-lateral, and (i) reduction in structural complexity of E-lateral tooth.

Characters listed for Helicinidae also characterize the subfamily Helicininae. In the following two subfamilies, Hendersoniinae and Vianinae, only characters that differ from the Helicininae are given.

Subfamily HENDERSONIINAE Baker, 1926a,  
REDEFINED

*Type-genus: Hendersonia* Wagner, 1905.

(For anatomical data see Baker, 1925.)

SHELL: (1) operculum paucispiral; (3) shell marked with radial sculpture. EXTERNAL ANATOMY: (7) axial cleft about 1 whorl long; (8) heart with two functional, unequal-sized auricles, right auricle almost vestigial; (11) hypobranchial duct short, opening into posterior end of mantle cavity. REPRODUCTIVE SYSTEM: (15) egg sac present at origin of primary oviduct; (16) primary gonoduct moderately long; (18) accessory sperm sac consisting of several small bulbs on left side of

pedicel opposite ascending limb of V-organ. RADULA: (20) A-, B-, and C-laterals with several cusps each; (22) accessory plate (E-lateral) with broad wing enveloping end of D-lateral; (23) innermost marginal teeth with three cusps, outer marginals polycuspid.

Subfamily VIANINAE Baker, 1922,  
REDEFINED

*Type-genus: Viana* H. and A. Adams, 1856.

(For anatomical data see Isenkrahe, 1867; Baker, 1926a.)

EXTERNAL ANATOMY: (6) tentacles short and conical in shape; (9) kidney narrowly crescent-shaped; (11) hypobranchial duct less than half length of pallial gonoduct. REPRODUCTIVE SYSTEM: (16) primary gonoduct long. RADULA: (20) A-, B-, and C-lateral teeth usually without cusps; (21) capituliform complex consisting of a T-lateral (D-lateral) and accessory plate (E-lateral); (22) accessory plate (E-lateral) reduced in size, without wing; (23) innermost marginal teeth unicuspid, outer marginals with one or few cusps.

#### FAMILY COMPARISONS

Numbers in parentheses refer to the characteristics given for the families Ceresidae and Proserpinidae. These two families are alike in only seven characteristics: (1) they lack opercula, (6) the tentacles, (13) the opening of the vagina into the mantle cavity, (14) the size and shape of the gonad, (15) the presence of an egg sac on the primary oviduct, (16) the structure of the primary gonoduct, and (18) the location of the accessory sperm sac. They differ in sixteen traits: (2) the periostracum, (3) shell sculpture, (4) the foot structure, (5) the mantle collar, (7) the axial cleft, (8) the number of auricles on the heart, (9) the structure of the kidney, (10), the location of the hypobranchial gland, (11) the length of the hypobranchial duct, (12) the openings of the pallial gonoduct and rectum, (17) the structure of the prostate, (19) the presence of a crystalline gland, and (20–23) all aspects of the radula.

Ceresidae and Helicinidae. The two families are alike in twelve characteristics: (2) the periostracum, (3) shell sculpture, (4) the foot structure, (5) the mantle collar, (6) the tentacles (except Vianinae), (10) the location of the hypobranchial gland (except Hender-

soniinae), (12) the openings of the rectum and pallial gonoduct, (19) the absence of a crystalline gland, and (20–23) similar radula (except Vianinae). The two families differ in eleven characteristics: (1) the presence of an operculum, (7) the axial cleft, (8) the number of auricles (except Hendersoniinae), (9) the structure of the kidney, (11) the length of the hypobranchial duct, (13) the opening of the vagina, (14) the size and shape of the gonad, (15) the presence of an egg sac, (16) the structure of the primary gonoduct, (17) the structure of the prostate, and (18) the location of the accessory sperm sac.

Proserpinidae and Helicinidae. The two families are alike in eleven characteristics. Five are shared with only the Hendersoniinae. Similarities are: (6) the tentacles (except Vianinae), (7) the axial cleft (Hendersoniinae only), (8) the auricles (except Hendersoniinae), (9) the structure of the kidney, (10) the location of the hypobranchial gland (Hendersoniinae only), (11) the length of the hypobranchial duct (Hendersoniinae only), (12) the openings of the rectum and pallial gonoduct (Hendersoniinae only), and (20–23) the structure of the radula (Vianinae only). The two families differ in nineteen traits: (1) the presence of an operculum, (2) shell sculpture, (4) the foot structure, (5) the mantle collar, (7) the length of the axial cleft, (10) the location of the hypobranchial gland, (11) the length of the hypobranchial duct, (12) the openings of the rectum and the pallial gonoduct, (13) the opening of the vagina, (14) the size and shape of the gonad, (15) the presence of an egg sac, (16) the structure of the primary gonoduct, (17) the presence of a prostatic provaginal sac, (18) the location of the accessory sperm sac, (19) the presence of a crystalline gland, and (20–23) all characteristics of the radula (except Vianinae).

From the foregoing data it is clear that the Ceresidae and the Proserpinidae are less closely related to each other than either is to the Helicinidae. Furthermore, recognition of the three groups as separate families is warranted by the degree of evolutionary divergence that has occurred.

The traits that are characteristic of the Ceresidae are primitive morphological states; whereas the traits unique to the Proserpinidae are advanced (derived) morphological states. The traits unique to Helicinidae indicate that it is also an advanced group compared to the Ceresidae but not to the same degree nor in the same lineage as is the Proserpinidae.

Morphological traits indicating these phylogenetic relationships are as follows: The ceresid right auricle is functional and only slightly reduced in size. It persists in the Hendersoniinae as a small, functional vestige. It is completely absent in other heliciniids and proserpinids. The ceresid (left) kidney is large and ovate. In the other families it is reduced in size and is crescent-shaped. The vestige of the right kidney (provaginal sac) persists in both sexes in the Proserpinidae. The provaginal sac persists only in females in the other two families. The vagina opens directly into the posterior corner of the mantle cavity in the Ceresidae and the Proserpinidae. In the Helicinidae it is incorporated into the hypobranchial duct. In Ceresidae the gonad is large and ovate, an egg sac is formed at the base of the primary gonoduct, and the accessory sperm sac is located on the left side of the pedicel. With regard to the opening of the vagina, the size of the gonad, the presence of an egg sac, and the location of the accessory sperm sac, the Proserpinidae are similar to the Ceresidae in retention of primitive characters as compared to the Helicinidae. In the Helicinidae the gonad is reduced in size, an egg sac is absent, and the accessory sperm sac is translocated to the right side of the pedicel (except in *Hendersonia*). In the Ceresidae the prostate is undivided. In the other two families it is divided into prostate-I and prostate-II. In addition, the Proserpinidae has evolved a crystalline gland, de novo, at the base of the reception chamber. The ceresid radula is generalized in all its traits. The central field teeth are heavily cusped, all the marginal teeth are multicusped, and the capituliform complex has a generalized comb-lateral and accessory plate. In Helicinidae a complete transition occurs in cusp reduction, transformation of the comb-lateral to a T-lateral, and simplification of the accessory plate. In the Proserpinidae these changes also are completed.

Similarities between the proserpinid and the vianid radula apparently are due to convergence, for little morphological similarity otherwise exists between the two groups. On the contrary, greater morphological similarity exists between the proserpinids and the

hendersoniines than between the proserpinids and other groups. The traits unique to the Ceresidae, Proserpinidae and Helicinidae necessitate recognizing these groups as distinct families. The aulacopod foot and the crystalline gland of the Proserpinidae are sufficient reasons for separating that family and indicate an extensive degree of divergence from the other two families.

MINOR TAXA AND SYSTEMATIC OBSERVATIONS

CERESIDAE Thompson, 1980

*Type-genus: Ceres* Gray, 1856.

The Ceresidae are known only from Mexico and South America and contain five genera. *Ceres* is the only genus that is known anatomically. The radula of *Linidiella* has also been described. It is like the radula of *Ceres* and unlike the radula of the West Indian Proserpinidae. On the basis of shell structure *Linidiella* is most similar to *Proserpina*, but a close relationship (family) between the two is not tenable on the basis of their radular differences. Thus *Linidiella* is tentatively referred to Ceresidae. The other three mainland genera are also provisionally assigned to Ceresidae because their shells are more similar in structure to *Linidiella* than to *Proserpina*. Because the radula of *Linidiella* is a generalized type of helicincean radula, similarities to *Ceres* may only indicate a generalized relationship within the Helicinacea. Additional anatomical data on the South American genera may necessitate further division at the family or subfamily level. *Dimorphoptychia* from the Paleocene of Europe has shell characters that could place it in the Ceresidae. Wenz (1938: 435) places it in a separate subfamily, the Dimorphoptychinae. Since *Dimorphoptychia* is known only as a fossil shell, speculation about its relationship to modern groups is highly arbitrary. I find no advantage in uniting it in the same family with *Ceres*, because shell characters are not absolutely useful for showing relationships among modern families (e.g., *Proserpina* and *Linidiella*).

KEY TO THE GENERA OF CERESIDAE

- 1) Shell 15–25 mm in major diameter; rugosely sculptured above, striate below; strongly keeled at periphery; with six apertural lamellae—two parietal, one columellar and three palatal ..... *Ceres*



- 1a) Shell seldom over 15 mm in major diameter; sculptured with weak growth striations and occasionally microscopic granules or punctations; periphery rounded; aperture with 0–2 lamellae confined to columella and/or parietal wall ..... 2
- 2) Aperture with two lamellae, one on parietal wall and one on base of columella . *Staffola*
- 2a) Aperture with fewer than two lamellae ..... 3
- 3) Aperture without lamella, although a small denticle may be present on base of columella .  
..... *Archecharax* n.g.
- 3a) Aperture with single lamella ..... 4
- 4) Lamella confined to columella ..... *Linidiella*
- 4a) Lamella confined to parietal wall ..... *Proserpinella*

*Ceres* Gray, 1856

*Ceres* Gray, 1856: 100. Type-species: *Carocolla eolina* Duclos, 1834, by subsequent designation (Kobelt, 1879: 203).

The shell is characterized by having six lamellae within the aperture: two parietal, one columellar, and three palatal. The shell is strongly keeled, has rugose sculpture on the spire and bears strong growth striations below. Three species have been described from eastern Mexico. The anatomy of one, *C. nelsoni*, and the radula of another, *C. salleana*, are described earlier in this paper.

*Ceres eolina* (Duclos)

*Carocolla eolina* Duclos, 1834: pl. 30.  
*Odontostoma (Carocolla) eolinum* (Duclos), Pfeiffer, 1848: 11.  
*Proserpina eolina* (Duclos), Pfeiffer, 1853: 290; Martens, 1890: 44; Martens, 1901: 609.  
*Ceres eolina* (Duclos), Gray, 1856: 102; Pfeiffer, 1856: pl. 35, figs. 23, 24.

*Type-locality*: State of Veracruz, Mexico.

*Distribution*: Mexico, Veracruz: Cerro de Palma, Sierra de Matlaquihahuitl, near Toxpan (Martens, 1901: 609). This is the only locality recorded for this species.

*Ceres nelsoni* Dall

*Ceres nelsoni* Dall, 1898: 27–28; Dall, 1902: 501, pl. 28, figs. 1, 3, 5, 8; Solem, 1954: 7.

*Type-locality*: Pilitla [Xilitla], San Luis Potosí, Mexico.

*Distribution*: Known only from the states of San Luis Potosí and Tamaulipas in eastern Mexico. Specimens examined.—San Luis

Potosí: Sotano del Rancho de la Barranca, 5 km NNE Ahuacatlan (UF 24404—1 shell, UF 24405—6 preserved animals); Sotano de Guadalupe, 10 km SW Aquismon (UF 24406—5 preserved animals, UF 24903—1 shell); 19 km E Xilitla, 350 m alt. (UF 24091a—1 preserved animal, UF 24901—19 shells, UF 24902—5 shells); 10 km NE Xilitla, 300 m alt. (UF 24900—5 shells); 12 km E Xilitla, 730 m alt (UF 24899—1 shell). Tamaulipas: Solem (1954: 7) records this species from Aserradero del Paraiso, 15 km NNW Chamla (UMMZ<sup>2</sup>).

*Ceres salleana* Gray

*Ceres salleana* Gray, 1856: 100–102; Pfeiffer, 1876: 295.

*Proserpina salleana* (Gray), Pfeiffer, 1856: 322, pl. 35, figs. 21, 22; Martens, 1890: 45.

*Type-locality*: Cordera [Cordova], Veracruz, Mexico.

*Distribution*: Known from localities immediately near the type-locality in Veracruz, Mexico: Orizaba; Cerro de Palma, Sierra de Matlaquihahuitl, near Toxpan (Martens, 1901: 609); Barranca de las Puentes (Martens, 1890: 45).

*Staffola* Dall, 1905

*Staffola* Dall, 1905: 202. Type-species by monotypy: *Proserpina (Staffola) derbyi* Dall, 1905.

*Staffola* is a monotypic genus which is characterized among ceresids by having two lamellae, one on the parietal wall and one projecting downward from the base of the columella. Sculpture consists only of a few incremental striations. However, the only

<sup>2</sup>Museum of Zoology, University of Michigan.

known material of the genus consists of the eroded subfossil holotype of *S. derbyi* and details about the sculpture cannot be adequately determined. The base of the shell has a thin umbilical callus.

Keen et al. (1960: 1288) and Boss & Jacobson (1975a, 1975b) synonymized *Staffola* with *Cyane* (= *Archecharax*). Even though *S. derbyi* hitherto has been unfigured, Dall's description gives due notice to the columellar lamella and the parietal lamella, which immediately separates *Staffola*. It was for this reason that Dall proposed a subgeneric relationship between *Staffola* and *Proserpina*, but continued to recognize *Cyane* (= *Archecharax*) as a distinct genus.

Additional observations on the holotype of *S. derbyi* are necessary to characterize *Staffola* among other South American genera. The holotype of *S. derbyi* is redescribed and figured herein.

*Staffola derbyi* (Dall)

*Proserpina* (*Staffola*) *derbyi* Dall, 1905: 202.

*Type-locality*: Calcareous banks of the arroyo of the Rio Chico at Paraguassa, State of Bahia, Brazil; holotype: USNM<sup>3</sup> 185454.

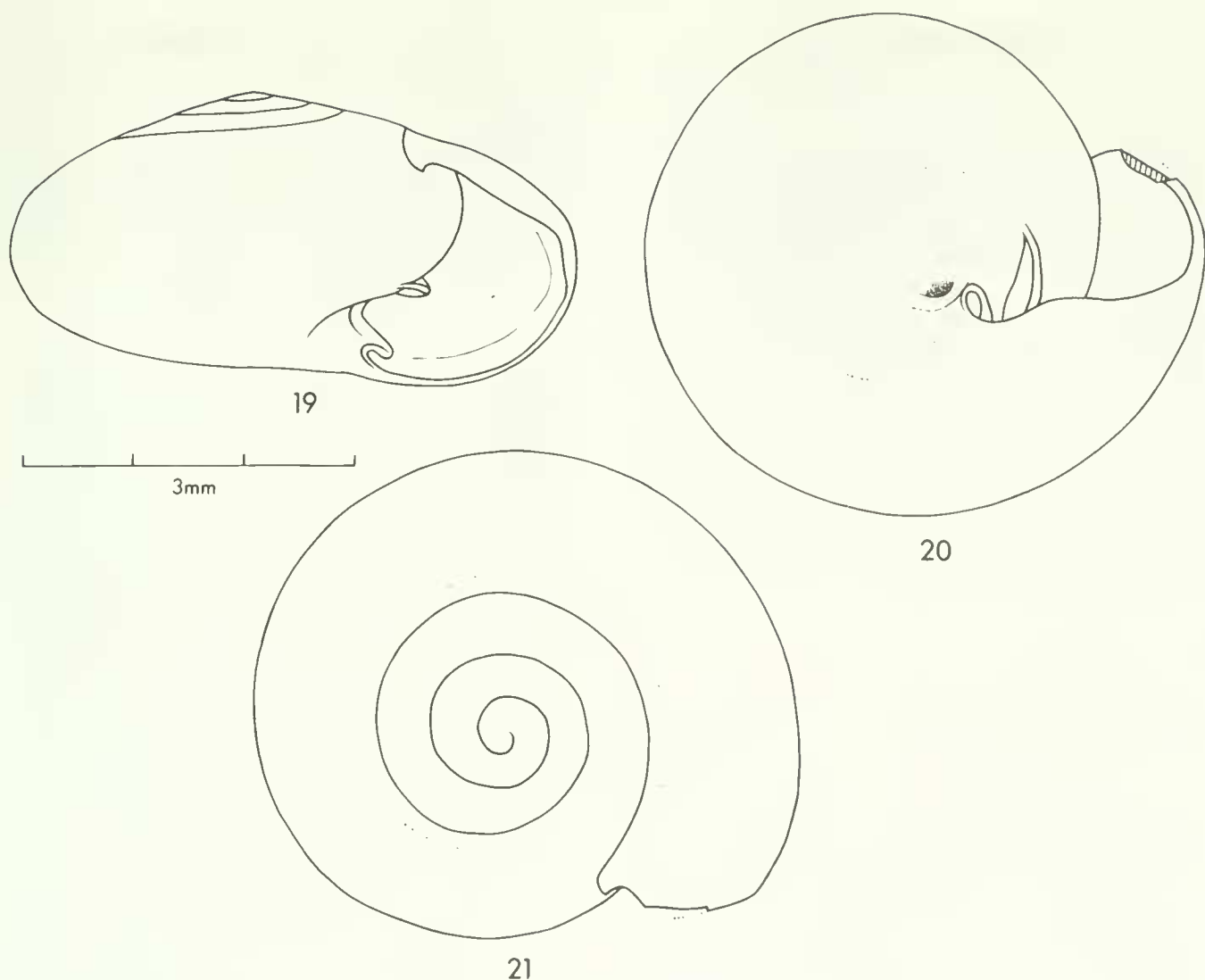
*Shell* (Figs. 19–21): 4.9 mm in major diameter; depressed globose, being about 0.55 times as high as wide. Spire weakly convex in outline with sharply pointed apex. Apical whorl slightly raised above succeeding whorl. Shell very thick for its size, strongly callused internally along peristome. Whorls 4.0. Suture not impressed, vaguely apparent along last whorl. Thin callus superimposed on suture forming a rather uniformly narrow spiral band. Body whorl nearly uniformly rounded peripherally but with tendency to flatten below periphery. Details of surface sculpture of holotype not clear due to weathered condition of shell, but few weak incremental growth wrinkles parallel to peristome distinguishable on shoulder of last eighth whorl. Base of shell with thin umbilical callus extending out as far as parietal lamella. Callus bearing weak minute granules, most of which are eroded. Umbilical region indented due to abrupt vertical descent of columellar wall of last eighth whorl. Aperture semilunar, with parietal and columellar lamella. Parietal lamella relatively thick and low, about one-eighth whorl long and lying about a third of distance from col-

umella to posterior angle of aperture. Columellar lamella projecting obliquely downward as tongue-like projection from columella, continuing into shell for about eighth whorl, and forming narrow bay-like notch at base of columella. Columella oblique in frontal view, ridged above and curved forward at base. Dorsal lip deeply indented near suture. Outer lip receding basolaterally, as does basal lip near columella. Peristome sharp-edged but with strong internal callus.

*Remarks*: This species is unusual because of its thick shell. No other ceresid approaches the condition that occurs in *S. derbyi*. Inasmuch as all ceresids live on calcareous rocks, the thickness of the shell in this case cannot be attributed to a factor of the habitat, but almost certainly is intrinsic. Another peculiarity of the species is the strongly receded dorsal lip that forms a distinct notch near its insertion with the preceding whorl. The depth of the notch is partially obscured in the holotype because the edge of the lip just outside the notch is broken. In Fig. 21 this is reconstructed on the basis of the curvature of the adjacent non-broken parts of the lip. The holotype of *S. derbyi* is eroded to the extent that the surface sculpture and details are obscured, and the outline of the suture is only apparent. My figure shows the course of the superimposed callus and not the underlying suture. It is notable that there is no perceptible impression of a suture. Other ceresids have at least a weakly impressed suture separating the whorls.

*S. derbyi* diverges strongly from other species in the structure of the apertural lamellae. It is unique among South American ceresids in possessing a parietal lamella, or to put it another way, *Linidiella* and *Archecharax* are unique by lacking a parietal lamella. The columellar lamella is dissimilar in its basic features to other ceresid genera. In contrast with other genera, the columellar lamella projects obliquely downward as an extension of the columella and forms a narrow U-shaped notch with the basal lip. The lamella resembles a tongue-like projection from the columella and curves into the aperture for about a quarter of a whorl. It appears to be a derivation from the truncate columellar condition such as occurs in *Archecharax*. It has little similarity to the columellar lamella of *Linidiella* or *Proserpina*, in which genera the columella tapers into the basal lip, and the lamella lies at

<sup>3</sup>National Museum of Natural History, Washington D.C.



FIGS. 19–21. *Staffola derbyi* (Dall). (Holotype: USNM 185454).

a right angle on the columella about a third of the distance from the parietal wall to the basal lip. Apparently the columellar lamella of *Staffola*, *Linidiella* and *Proserpina* are independently derived, representing cases of convergent evolution in this structure.

*Linidiella* Jousseume, 1889

*Linidiella* Jousseume, 1889: 256; Baker, 1923: 84. Type-species by subsequent designation (Baker, 1923: 84): *Proserpina swifti* Bland, 1863.

*Chersodespoena* Sykes, 1900: 136. Type-species by original designation: *Despoena* (*Chersodespoena*) *cinnamomea* Sykes, 1900.

Shell with single lamella at base of columella. Columella concave, thickened, and grading into lamella. Sculpture consisting of fine, irregularly spaced incremental striations that become more distinct on periphery and base. Interspersed between striations on base

of shell are numerous minute elongate granules which become more concentrated near umbilical region. Umbilical callus not evident; indicated at best by concentrated granular sculpture. Dorsal surface of shell lacking granular or punctate sculpture. Enamel deposit overlapping suture to form spiral line lying about midway between sutures. The radula is discussed earlier in this paper.

*Linidiella* contains three species. Two are from the Andes of northern South America and one is from Chiapas, Mexico. They are placed together in *Linidiella* because each has a spiral lamella at the base of the columella. I suspect that the similarity among the species based on this character is superficial and that two separate lineages are represented. *L. sulfureous* from Chiapas differs significantly from the two Andean species in that its shell is nearly devoid of granular sculpture, and incremental striations are hardly distinguishable. The species are as follows: each is known certainly only from its type locality.

*Linidiella swifti* (Bland)

*Proserpina swifti* Bland, 1863: 16–17; Bland, 1865: 155, fig. 1.

*Cyane swifti* (Bland), Thiele, 1927: 90, fig. 65.

*Type-locality*: mountains between Puerto Cabello and Valencia, Venezuela.

Miller (1879: 148) listed this species from "Ecuador" on the basis of specimens obtained by Higgins. Aside from this record the species is known only from the type-locality. The specimens that I have examined (UF 19053) are merely labeled "Venezuela." They came from C. T. Simpson and may have been received from Thomas Swift, who originally discovered this species. These specimens are figured (Figs. 22–23) to contrast *Linidiella* with *Staffola* and *Archecharax*.

*Linidiella cinnamomea* (Sykes)

*Despoena (Chersodespoena) cinnamomea* Sykes, 1900: 136–137, fig.

*Type-locality*: between Ayabamba and Santa Rosa, Ecuador.

*Linidiella sulfureous* Thompson

*Linidiella sulfureous* Thompson, 1967: 61, figs. 1–3.

*Type-locality*: 8.2 mi. S. Solusuchiapa, Chiapas, Mexico; 1600 ft. alt.

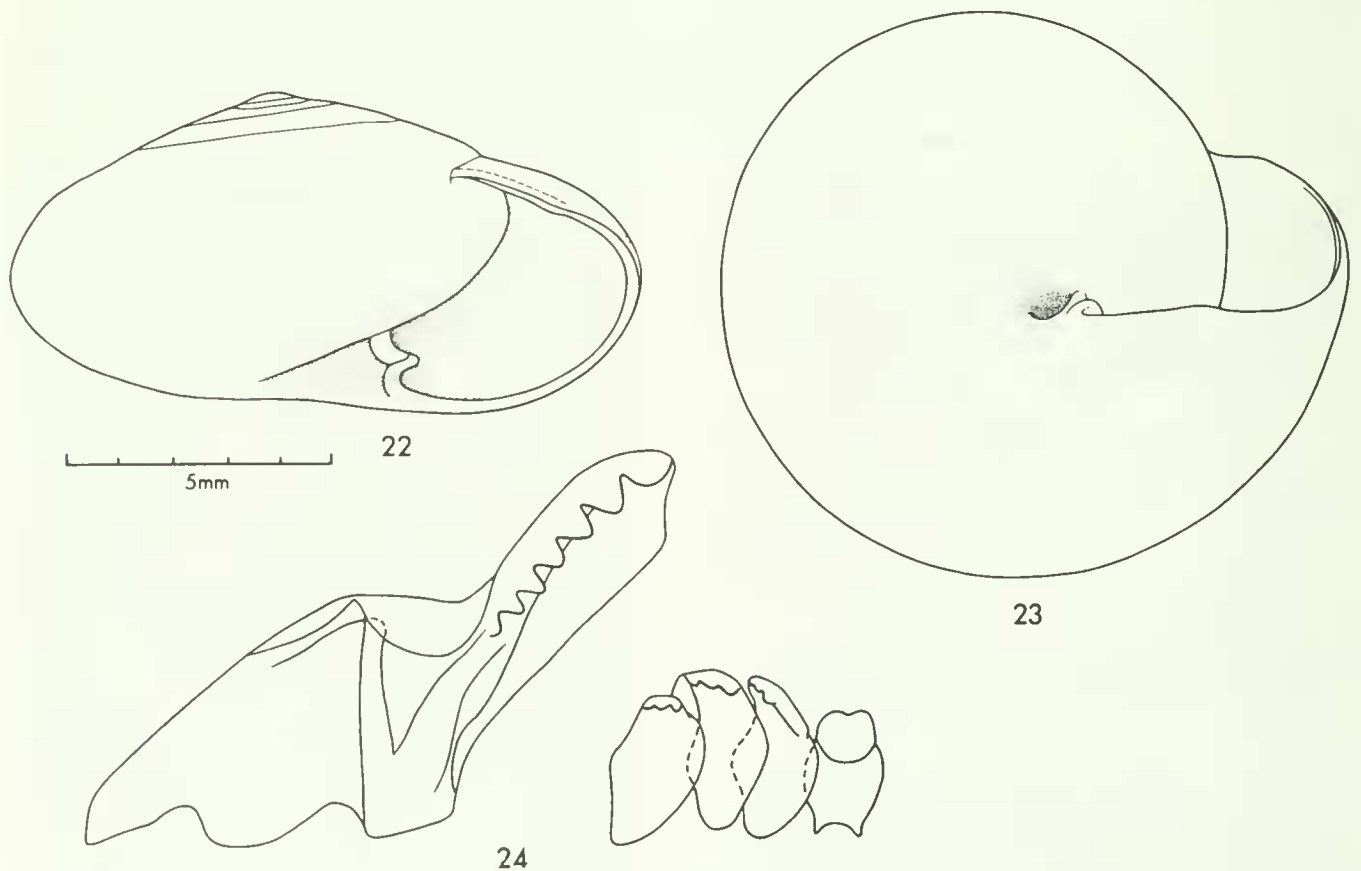
*Archecharax* Thompson,  
*new generic name*

*Cyane* H. Adams, 1870: 376. Non *Cyane* Felder, 1861; Lepidoptera.

*Type-species*: *Cyane blandiana* H. Adams, 1870.

*Etymology*: The name *Archecharax* is derived from the Greek *arche*, first cause, and *charax*, a pointed stake. It alludes to the structure of the columella. The name is masculine.

A genus of the family Ceresidae with the following characteristics (all aspects of its soft anatomy are unknown). Aperture lacking internal lamella; columella truncate, may project forward basally as denticle; periostracum absent. Sculpture particularly noticeable on base and side of whorls, consisting of rather



FIGS. 22–24. *Linidiella swifti* (Bland). Figs. 22–23. Two specimens from Simpson Collection (UF 19053). Fig. 24. Radula redrawn from Thiele, 1931: 90.

regularly spaced incremental striations between and within which numerous small granules occur in radial patterns.

*Archecharax* is immediately distinguishable from other ceresids and proserpinids by having a truncate columella and lacking lamellae within the aperture. Equally striking is the presence of regularly spaced growth striations

and radially arranged granular tubercles on the base and sides of the whorls outside the basal callus.

*Archecharax* is known from the foothills and outer mountain ranges of the Andes from Colombia south to Bolivia. Four extant species are described. These may be separated by the following key:

KEY TO THE SPECIES OF *ARCHECHARAX*

- 1) Dorsal and ventral surface with conspicuous spiral rows of punctate sculpture ..... *A. blandianus* (H. Adams)
- 1a) Shell without spiral or punctate sculpture ..... 2
- 2) Shell large, 13–15 mm in major diameter; depressed, less than 0.55 times as high as wide ..... 3
- 2a) Shell smaller, less than 10 mm in major diameter; conic-globose, more than 0.60 times as high as wide ..... *A. orbignyi* (Ancy)
- 3) Shell yellowish with red spiral band about midway between suture and periphery; spire weakly convex in outline ..... *A. cousini* (Jousseume)
- 3a) Shell uniformly amber colored; spire weakly concave in outline .*A. glaeserius* new species

*Archecharax blandianus* (H. Adams)

*Cyane blandiana* H. Adams, 1870: 376; pl. 27, figs. 2, 2a.

*Type-locality*: "Eastern Peru."

This species has not been recorded since its discovery. Its original description and figures are deficient in some details. It is described and figures herein based upon material I collected in 1969.

*Shell* (Figs. 25–27): Depressed-helicoid, about 10 mm in major diameter and about 0.59–0.69 times as high as wide. Largest specimen examined with about 5.3 whorls (UF 24359). Spire weakly concave in outline; apex rounded. Body whorl slightly swollen, evenly rounded at periphery; base moderately convex. Suture weakly impressed on last two whorls, not at all on earlier whorls. Umbilicus imperforate, but with a dimple-like impression that lies behind the columellar insertion. Periphery of impression rather abrupt. Protoconch consisting of 0.6 whorl, set off by a distinct transverse crease. First half whorl of protoconch smooth, subsequent 0.1 whorl with a few weak radial striations; following whorls with incremental striations, within and between which are close spiral striations that may be broken into short linear segments or rows of shallow punctations (Figs. 31, 32). Spiral sculpture most conspicuous near su-

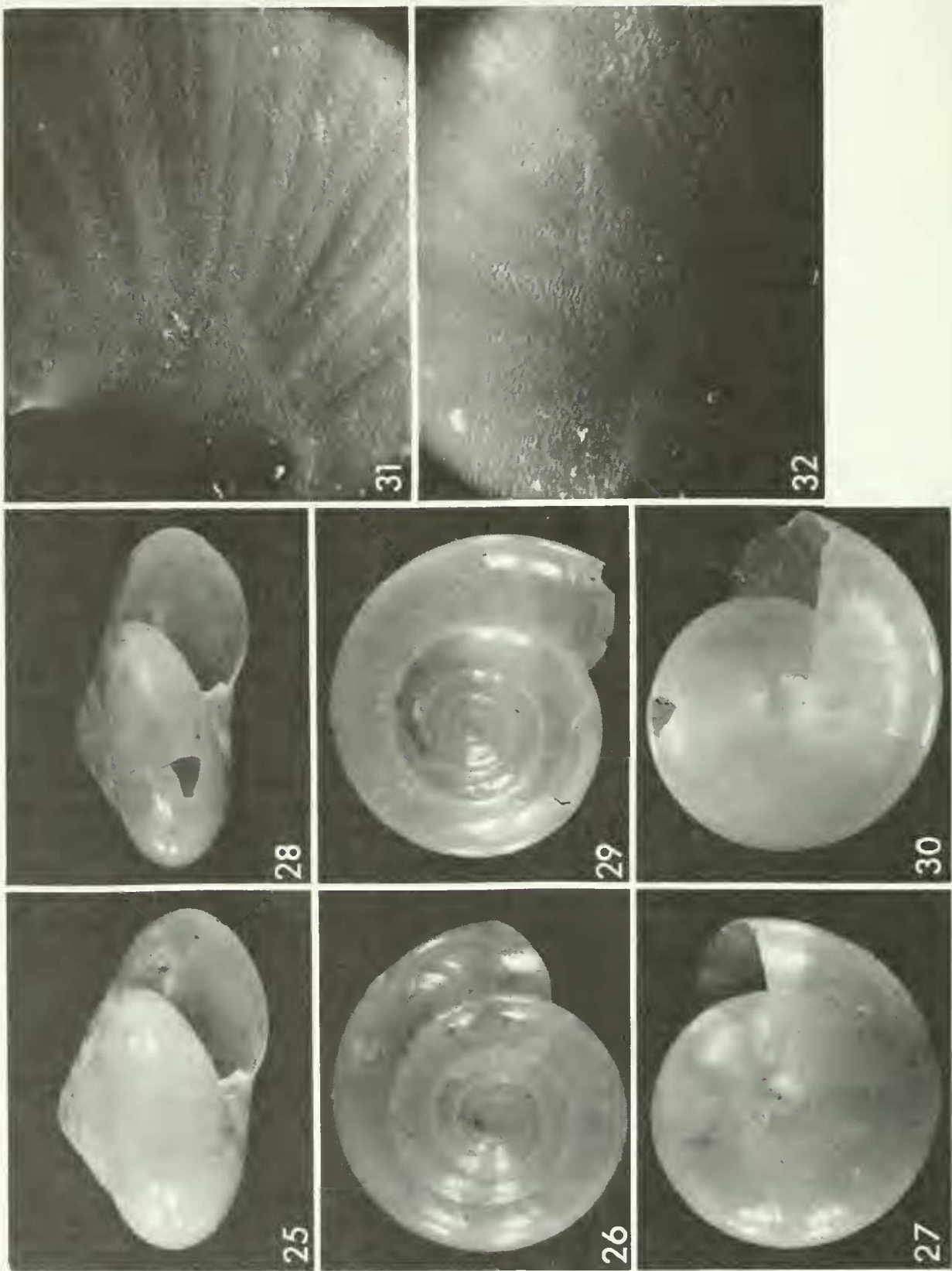
ture and on base, weakest around periphery (Fig. 27). Parietal area without apparent callus or deposit; spiral sculpture continuing into aperture undiminished. Aperture semi-lunar; without lamellae. Columella conspicuously thickened, concave and slightly twisted at base, forming very weak forward-projecting denticle. Dorsal lip extending forward and inserted well above periphery of preceding whorl. Outer lip and basal lip nearly straight in lateral profile.

Size is highly variable. Measurements in mm for the five largest specimens examined are:

			Aperture		Whorls
	Width	Height	Width	Height	
UF 24355	7.0	4.6	3.2	3.1	5.0
UF 24356	7.7	5.1	3.8	4.0	4.6
UF 24357	5.8	4.0	2.6	2.6	4.7
UF 24358	9.8	6.2	4.8	4.2	5.2
UF 24359	7.3	4.3	3.3	2.8	5.0

*Distribution*: Known only from eastern Peru in vicinity of Tingo Maria. This is a region of extensive limestone karst formations.

*Specimens examined*: Peru: Huanuco Province; Tingo Maria, 750 m alt. (UF 24356.5); 4.7 km S Tingo Maria, 750 m alt. (UF 24350.4); 9.2 km S Tingo Maria, 800 m alt. (UF 24357.1); 14.9 km NE Tingo Maria, 800 m alt. (UF 24358.2).



FIGS. 25-27. *Archecharax blandianus* (Adams) (UF 24359). FIGS. 28-30. *Archecharax glaeceus* new species (Holotype: UF 24355). FIGS. 31-32. *Archecharax blandianus* (Adams) (UF 24356). SEM of base just behind lip showing radial and granular sculpture. Fig. 31.  $\times 42.4$ , Fig. 32.  $\times 108$ .

*Remarks:* The distinct spiral punctate sculpture on the dorsal surface of the whorls in *A. blandianus* is different from the sculptural traits of any other related species, and on the basis of that character alone separate generic status for *A. blandianus* is justifiable. Perhaps the three other species that I assigned to *Archecharax* should be placed in a new subgenus because of the absence of such spiral sculpture. Until better material is available I prefer not to make such an allocation.

*Archecharax orbignyi* (Ancey)

*Cyane orbignyi* Ancey, 1892: 178.

*Type-locality:* Santa Cruz de la Sierra, Bolivia.

*Distribution:* known only from the type-locality.

*Archecharax cousini* (Jousseaume)

*Proserpinella cousini* Jousseaume, 1887: 181–182, pl. 3, figs. 15, 16.

*Type-locality:* "Ecuador."

*Distribution:* Ecuador, but not known from any precise locality.

*Archecharax glaeserius* Thompson, *new species*

*Type-locality:* Colombia, Departamento Valle, 3 km W Atoncelo, 1380 m alt., Holotype: UF 24355; collected 1 March 1969 by Fred G. Thompson. The type-locality is at the head of a deep ravine in a mountain rain forest near the top of a mountain range lying west of Dagua and Atoncelo. The unique holotype was found at the base of a huge calcareous sandstone boulder in the ravine.

*Shell* (Figs. 28–30, 33–36): major diameter about 16 mm; depressed helicoid, being about 0.54 times as high as wide. Spire elevated, slightly concave in profile due to expansion of last whorl. Periostracum absent. Shell opaque, glossy, amber yellow, except for white umbilical callus with regularly spaced, narrow darker yellow streaks paralleling line of growth, visible through surface gloss. Umbilical area with thin granular callus strongly indented immediately behind the columella due to abrupt vertical wall of last whorl at that point (Fig. 36). Whorls 4.7; suture moderately depressed and covered by thin glaze forming narrow transparent zone extending onto preceding whorl and partially obscuring suture. Glaze with numerous small

dimples and pits randomly dispersed over suture area. Protoconch with 1.0 whorl, smooth, elevated above succeeding whorl; very weakly set off from succeeding whorl by faint rest striation. Subsequent whorl smooth but with sparse, fine, incremental striations most noticeable on base and rarely distinguishable above. Microsculpture on base consisting of numerous minute granules tending to be aligned between incremental striations and arranged in a spiral course. Granules densest on basal callus and disappearing near periphery of whorl. Aperture 0.83 times as high as wide, deeply indented by preceding whorl. Lamella absent. Peristome simple, sharp; columella weakly concave, oblique; base truncate, extending forward as weak denticle accentuated by receding basal lip. Denticle does not continue internally as lamella but curves upward uniformly into columella.

Measurements in mm of the unique holotype are: width, 15.7; height, 8.4; aperture width, 7.0; aperture height, 5.8.

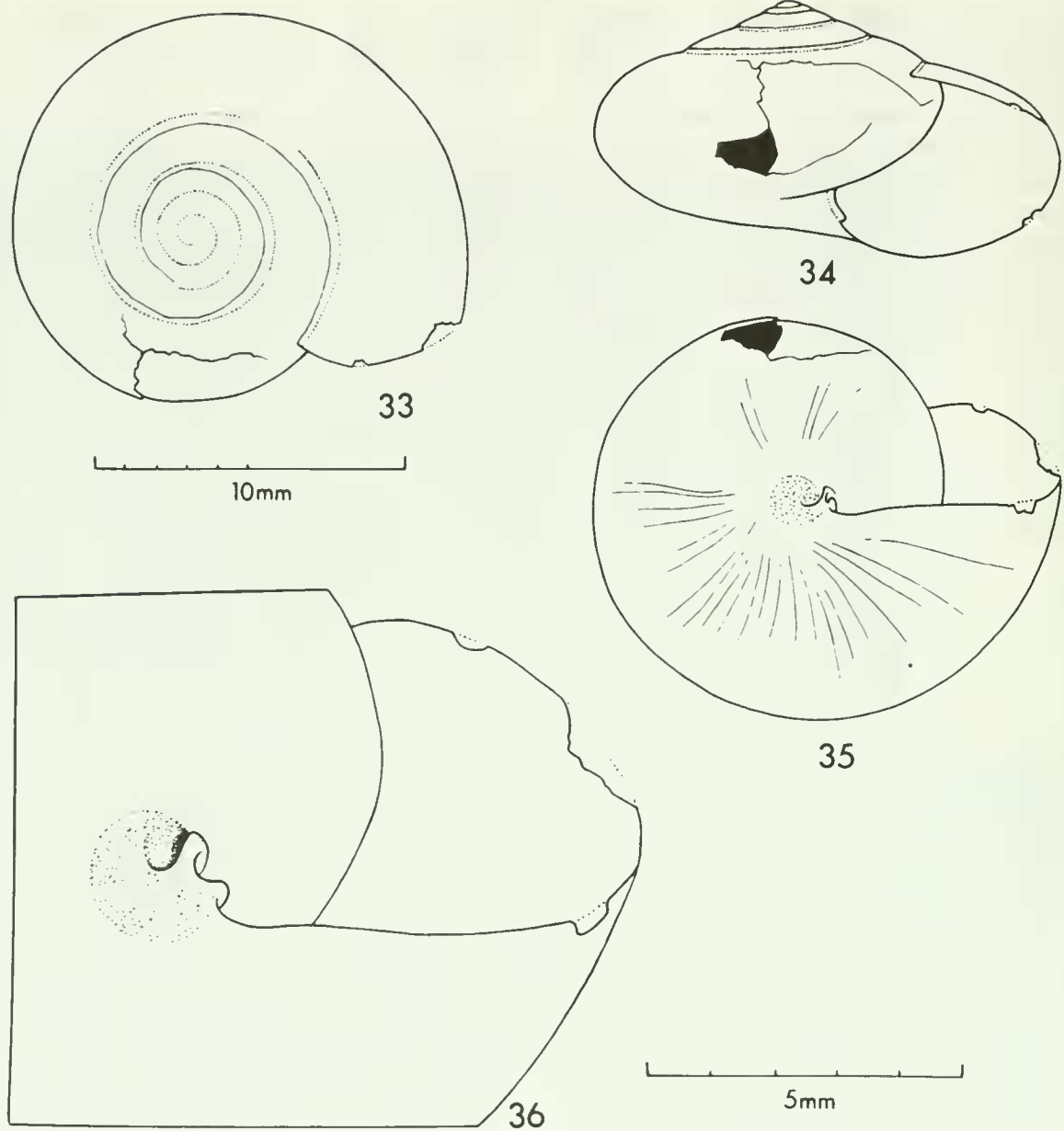
*Remarks:* The species is most similar in its shell characters to *A. cousini* (Jousseaume). Both species have a smooth spire devoid of spirally arranged rows of punctate sculpture, are similar in size and relative height, and both have a small denticle-like projection at the base of the columella. *A. glaeserius* is immediately separated from *A. cousini* by the color of its shell and the contour of its spire. *A. glaeserius* is uniform amber yellow and has a weakly concave spire. *A. cousini* possesses a red spiral band on a yellow background, and has a weakly convex spire.

*A. cousini* is known only from its holotype, for which Jousseaume gives only a brief description and an outline illustration. Apparently the relationship between *glaeserius* and *cousini* is close, but their differences are sufficient to consider them distinct species. Additional collections may show they are subspecifically related.

*Proserpinella* Bland

*Proserpinella* Bland, 1865: 157. Type-species by monotypy: *Proserpinella berendti* Bland, 1865.

The genus is characterized by having a smooth, discoidal shell that bears a delicate parietal lamella. Other lamellae are absent. The columella is truncate, similar to that in *Archecharax*. A thin umbilical callus is present.



FIGS. 33–36. *Archecharax glaeceus* new species (Holotype: UF 24355). Fig. 36. Enlargement showing detail of columellar area. 10 mm scale for 33–35, 5 mm scale for 36.

*Proserpinella* is an obscure genus of minute Mexican land snails; two species have been described. Nothing is known about them other than the descriptions of their shells. Each is known only from its type-locality.

*Proserpinella berendti* Bland

*Proserpinella berendti* Bland, 1865: 157, fig. 2; Strebel, 1873: 11, pl. 4, fig. 5; Martens, 1890: 45.

*Type-locality*: Mirador, Veracruz, Mexico, 3000–4000 ft alt.

*Proserpinella hanna*e Dall

*Proserpinella hanna*e Dall, 1926: 486–487, pl. 36, figs. 6–8.

*Type-locality*: Maria Madre Island, Tres Marias Islands, Nayarit, Mexico.

PROSERPINIDAE Gray, 1847

This family is endemic to the Greater Antillean Islands of Cuba, Jamaica, and Hispaniola, and contains two genus-group taxa, *Proserpina* Sowerby, 1847, and *Despoenella* Baker, 1923. Conventionally *Despoenella* is treated as a subgenus of *Proserpina*. Equally valid reasons can be given for treating it as a separate genus. For the purposes of this paper I follow previous authors and treat them as subgenera. However, recognition of them as subgenera or distinct genera on the basis of our current knowledge is subjective. *Proserpina* is characterized by having a columellar lamella, two parietal lamellae, and two



palatal lamellae. *Proserpina* is restricted to Jamaica and contains two species. *Despoenella* has a columellar lamella and a single parietal lamella. Palatal lamellae are absent. *Despoenella* contains two species each on Cuba and Jamaica and three on Hispaniola.

Until now the only information available dealing with internal anatomy is Baker's (1926b) description of the radula of *P. (Despoenella) depressa* (Orbigny), the type-species of *Despoenella*. Data on the soft anatomy of *P. nitida* Sowerby, the type-species of *Proserpina* are presented earlier in this paper. These data are the basis of characterizing the Proserpinidae as a distinct family. Two new species of *Despoenella* are also described. In view of the excellent monograph on the Proserpinidae by Boss & Jacobson (1975a), further discussion of most other species is not necessary.

*Calybium* from Southeast Asia may be a proserpinid, but it is only known from its shell and radula (see Baker, 1922: 64–65), and its relationship within the proserpinid-helicinid complex remains unclear.

### *Proserpina* Sowerby

#### Subgenus *Proserpina*, s.s.

*Proserpina* Sowerby, 1839: 124; Boss & Jacobson, 1975: 67–69. Type-species: *Proserpina nitida* Sowerby, 1839, by monotypy.

*Despoena* Newton, 1891: 255. New name for *Proserpina* Sowerby, 1839, non *Proserpinus* Hubner, 1816, Lepidoptera.

#### *Proserpina (Proserpina) nitida* Sowerby

*Proserpina nitida* Sowerby, 1839: 124, fig. 274; Boss & Jacobson, 1975a: 69–72, pl. 10, figs. 1–5.

*Proserpina nitida planulata* C. B. Adams, 1851: 174.

*Type-locality*: Jamaica.

*Distribution*: widely distributed throughout the central portion of Jamaica.

#### *Proserpina (Proserpina) linguifera* (Jonas)

*Helicina linguifera* Jonas, 1839.

*Proserpina allognoto* Jonas, 1846. New name for *Helicina linguifera* Jonas, 1839.

*Proserpina pulchra* C. B. Adams, 1850: 81.

*Proserpina linguifera* (Jonas), Pfeiffer, 1850: 12, pl. 103, figs. 12–15; Boss & Jacobson, 1975a: 72–74, pl. 10, figs. 6–7.

*Type-locality*: Jamaica.

*Distribution*: known only from St. Elizabeth Parish and Westmoreland Parish, Jamaica.

#### Subgenus *Despoenella* Baker

*Odontostoma* Orbigny, 1842: 238. Type-species: *Odontostoma depressa* Orbigny, 1842. Non *Odontostoma* Turton, 1830, Gastropoda.

*Despoenella* Baker, 1923: 85. New name for *Odontostoma* Orbigny, 1842, non *Odontostoma* Turton, 1830. Boss & Jacobson, 1975a: 74.

#### *Proserpina (Despoenella) globulosa* (Orbigny)

*Odontostoma globulosa* Orbigny, 1842: 239, pl. 18, figs. 8–11.

*Proserpina globulosa* (Orbigny), Pfeiffer, 1850: 12, pl. 12, figs. 19–21; Boss & Jacobson, 1975a: 84–87, pl. 13, figs. 4–6.

*Type-locality*: Interior of island of Cuba.

*Distribution*: Widely disjunct in its distribution in Oriente and Pinar del Rio Provinces, Cuba, and the Isle of Pines.

#### *Proserpina (Despoenella) pisum* C. B. Adams

*Proserpina pisum* C. B. Adams, 1850b: 108. Boss & Jacobson, 1975a: 82–84, pl. 13, figs. 103.

*Type-locality*: Jamaica.

*Distribution*: Confined to western Jamaica where it is found in Westmoreland, St. James, and Trelawny Parishes.

#### *Proserpina (Despoenella) depressa* (Orbigny)

*Odontostoma depressa* Orbigny, 1842: 238, pl. 18, figs. 4–7.

*Helicina ptychostoma* Pfeiffer, 1848: 12.

*Proserpina depressa* (Orbigny), Pfeiffer, 1853: 291; Baker, 1926b: 451 (radula); Boss & Jacobson, 1975a: 75–78, pl. 11, figs. 1–3.

*Proserpina depressa rubrocincta* (Torre, MS, Aguayo & Jaume, 1947: 88 (*nomen nudum*); Aguayo & Jaume, 1957: 124, pl. 1, fig. 10.

*Type-locality:* *Odontostoma depressa* Orbigny: interior of the isle of Cuba; restricted by Aguayo & Jaume (1947: 88) to Pan de Guajaiboa, Pinar del Rio, Cuba. *Helicina ptychostoma* Pfeiffer: Callajabas [=Caya-jabos], Pinar del Rio, Cuba. *Proserpina depressa rubrocincta* Aguayo & Jaume: Los Acostas, Luis Lazo, Pinar del Rio, Cuba.

*Distribution:* widely disjunct; confined to Pinar del Rio Province and Havana Province in western Cuba and Oriente Province in eastern Cuba.

*Proserpina (Despoenella) bidentata*  
C. B. Adams

*Proserpina bidentata* C. B. Adams, 1850a: 81; Boss & Jacobson, 1975a: 79–80; pl. 12, figs. 4–6.

*Type-locality:* Jamaica.

*Distribution:* confined to the John Crow Mountains, Portland Parish, Jamaica.

*Proserpina (Despoenella) marcanoi* Clench

*Proserpina marcanoi* Clench, 1962: 2, pl. 1, fig. 3; Boss & Jacobson, 1975a: 80–82, pl. 12, figs. 1–3.

*Type-locality:* Colonia Ramfis [=Colonia Majagual], 20 km W of San Cristobal. San Cristobal Province, Dominican Republic.

*Distribution:* known only from the type-locality.

*Remarks:* observations are given below with the following species.

*Proserpina (Despoenella) scudderæ*  
Thompson, *new species*

*Etymology:* this species is named for Sylvia Scudder, Technician, Florida State Museum, who assisted in field work in the Dominican Republic in 1974.

*Type-locality:* Dominican Republic, Barahona Prov., Sierra de Baoruco, 7 km NNE Polo, 910 m alt. The type-locality is in a deep limestone ravine. On my first visit in January 1974 the ravine was shaded by a wet mountain forest that was partly planted with coffee. At the time of the most recent visit (January 1977) the ravine was deforested along both sides with cattle pasture on the

north slope and open coffee grove on the south slope.

*Holotype:* UF 24326; collected 18 June 1974 by Fred G. Thompson.

*Paratypes:* UF 24327 (19), UF 24328 (25), UF 24329 (5), FMNH<sup>4</sup> 195426 (2), ANSP<sup>5</sup> (2), MCZ<sup>6</sup> 288377 (2). Museo Nacional de Historia Natural, Republica Dominicana (5). All paratypes are topotypic.

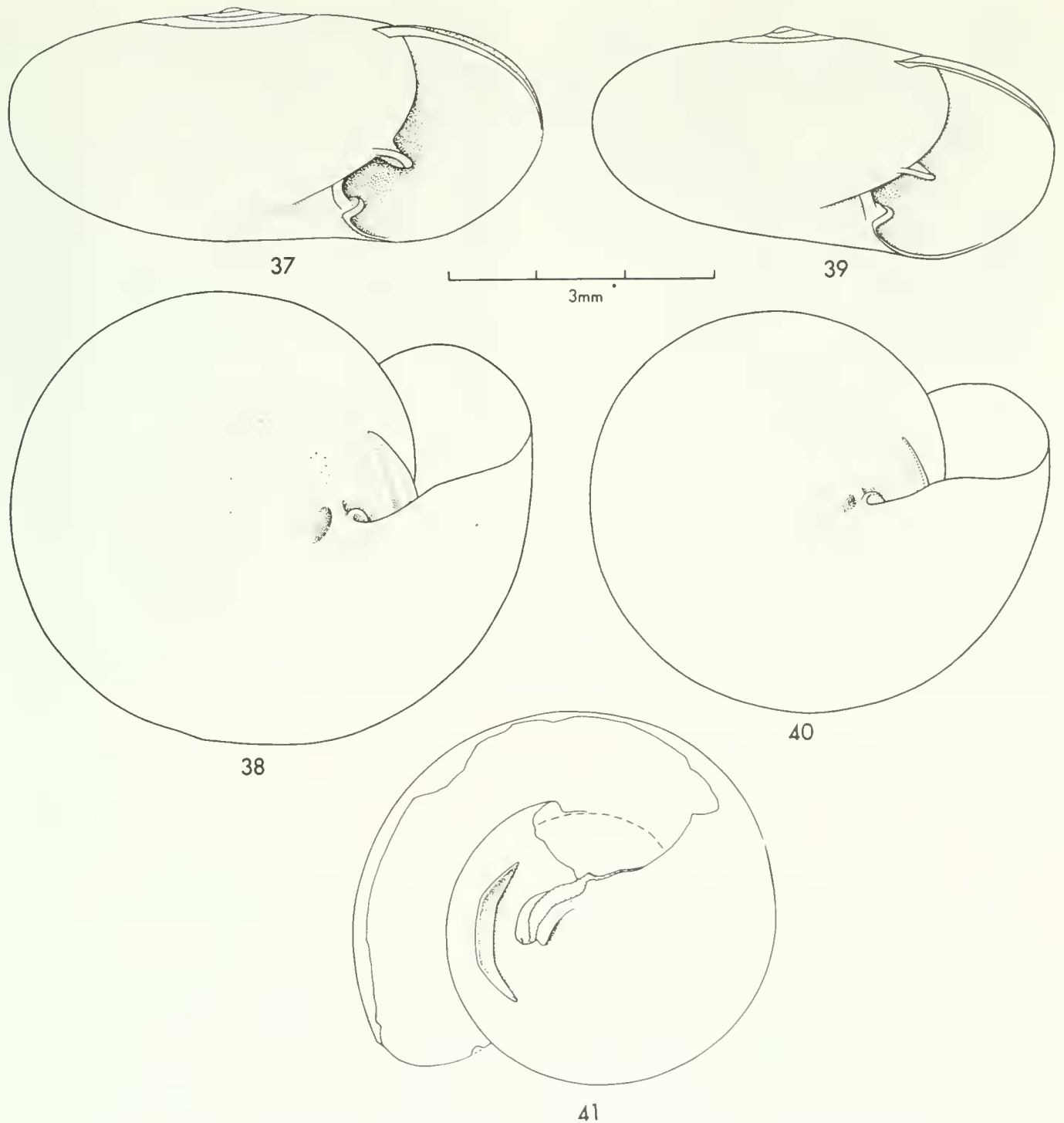
*Shell* (Figs. 37–41): small, 5.2–5.9 mm in diameter; discoidal, adult shells 0.47–0.49 times as high as wide (0.48 in holotype); whorls 4.5–5.0 (4.8 in holotype). Spire depressed. Embryonic whorl conspicuously protruding. Last whorl flattened above and rounded below so that periphery of shell lies above middle. Color light greenish-yellow dorsally, lighter below (only dead shells have been collected; live specimens probably are brighter green than the material I have examined). Surface of shell glossy with thin enamel-like wash that overlaps suture and extends about halfway onto previous whorl. Shell fairly translucent, showing regularly spaced, thin incremental lines of growth through outer wash. Dorsal surface and sides of whorls smooth. Ventral surface with thin white basal callus that is very minutely granular. Callus extending outward as arc continuing forward from parietal lamella. Columellar margin of umbilical area indented, forming short abrupt wall that causes base to be weakly pitted (Figs. 38, 40). Aperture semi-lunar, equal to or slightly higher than wide, 0.38–0.44 times width of shell (0.39 in holotype). Aperture with parietal lamella and columellar lamella, both extending into aperture about 1/5 whorl (Fig. 41). Parietal lamella located about third distance from columella to posterior angle of aperture. Columellar lamella located just above middle of columella and about half as high as parietal lamella. Lip strongly sinuous in outline, strongly receded at periphery and along base. Columella oblique, lying at about 30° to vertical axis of shell. Columella accentuating umbilical pit by having pillar-like thickening between parietal wall and columellar lamella.

Measurements of 12 specimens selected to show maximum variations (holotype in parentheses): height, 2.5–2.8 mm (2.7); width, 5.2–5.9 mm (5.6); aperture height, 2.1–2.4 mm (2.3); aperture width, 2.1–2.3 mm (2.2).

<sup>4</sup>Field Museum of Natural History, Chicago.

<sup>5</sup>Academy of Natural Sciences of Philadelphia.

<sup>6</sup>Museum of Comparative Zoology, Cambridge, Mass



FIGS. 37–41. *Proserpina (Despoenella) scudderæ* new species. Figs. 37–38. Large paratype (UF 24328). Figs. 39–40, small paratypes (UF 24328). Fig. 41. Paratype opened to show lamella (UF 24328).

*Distribution:* this snail has been found only in the Sierra de Baoruco, near Polo, Dominican Republic, where it was collected on limestone outcrops in wet forests. Records in addition to the type-locality are: 6 km NNE Polo, 1000 m alt. (UF 24332); 5 km NNE Polo, 990 m alt. (UF 24331); 2 km NNE Polo, 765 m alt. (UF 24333); 3 km SE Polo, 750 m alt. (UF 24330).

*Remarks:* this is a member of the subgenus *Despoenella* by virtue of possessing two lamellae within the aperture, a parietal lamella, and a columellar lamella. It differs

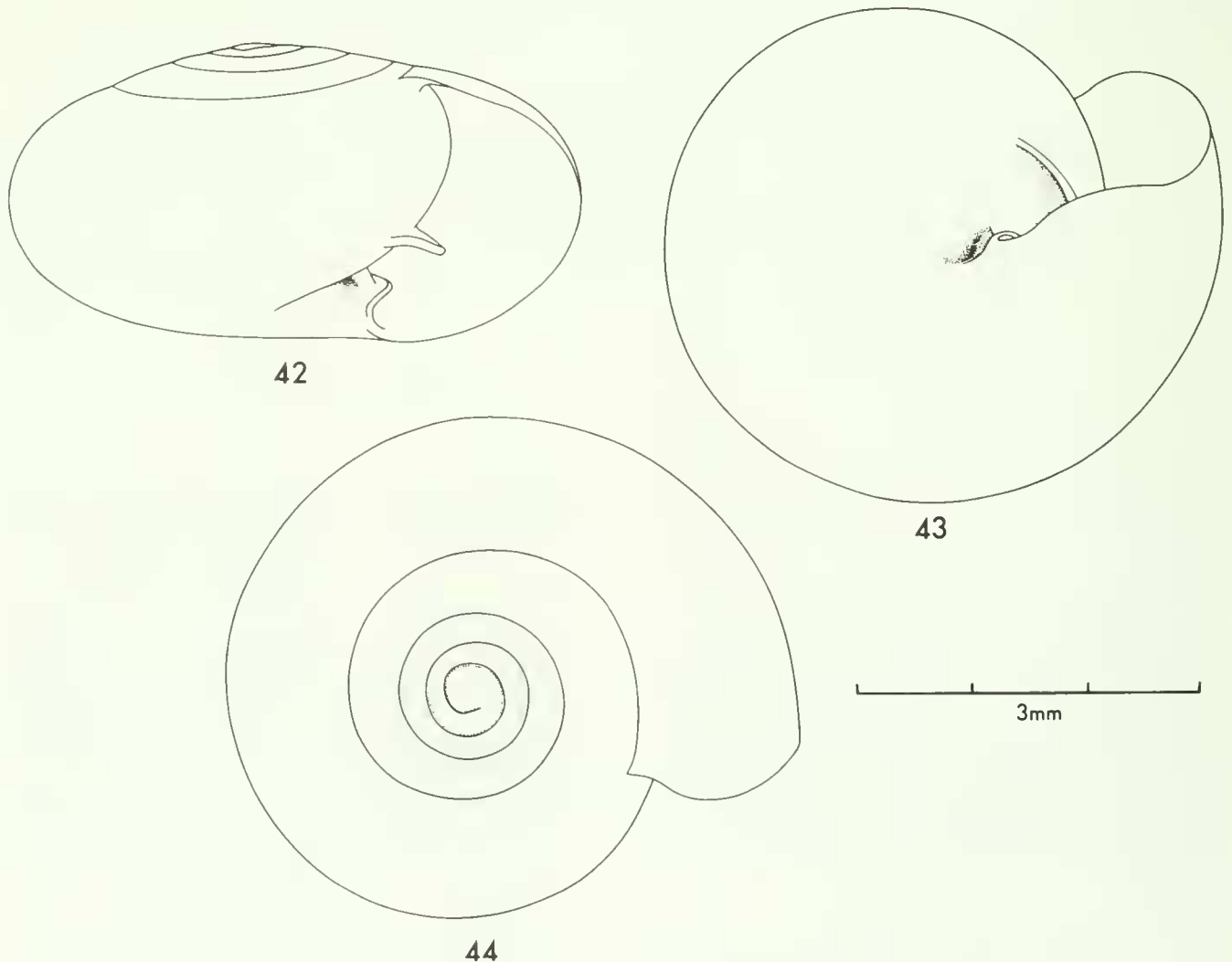
from most of its subcongeners by its discoidal shape and its protruding embryonic whorl. Its differences from *P. planior* are described below under that species. Adult shells are less than 0.50 times as high as wide with the periphery lying above the middle of the last whorl. Other species of *Despoenella*, except *P. planior*, are helicoid or depressed-helicoid in shape with the periphery of the shell lying at the middle of the last whorl, and the embryonic whorl is not conspicuously elevated above the succeeding whorls.

The subgenus *Despoenella* is divisible into

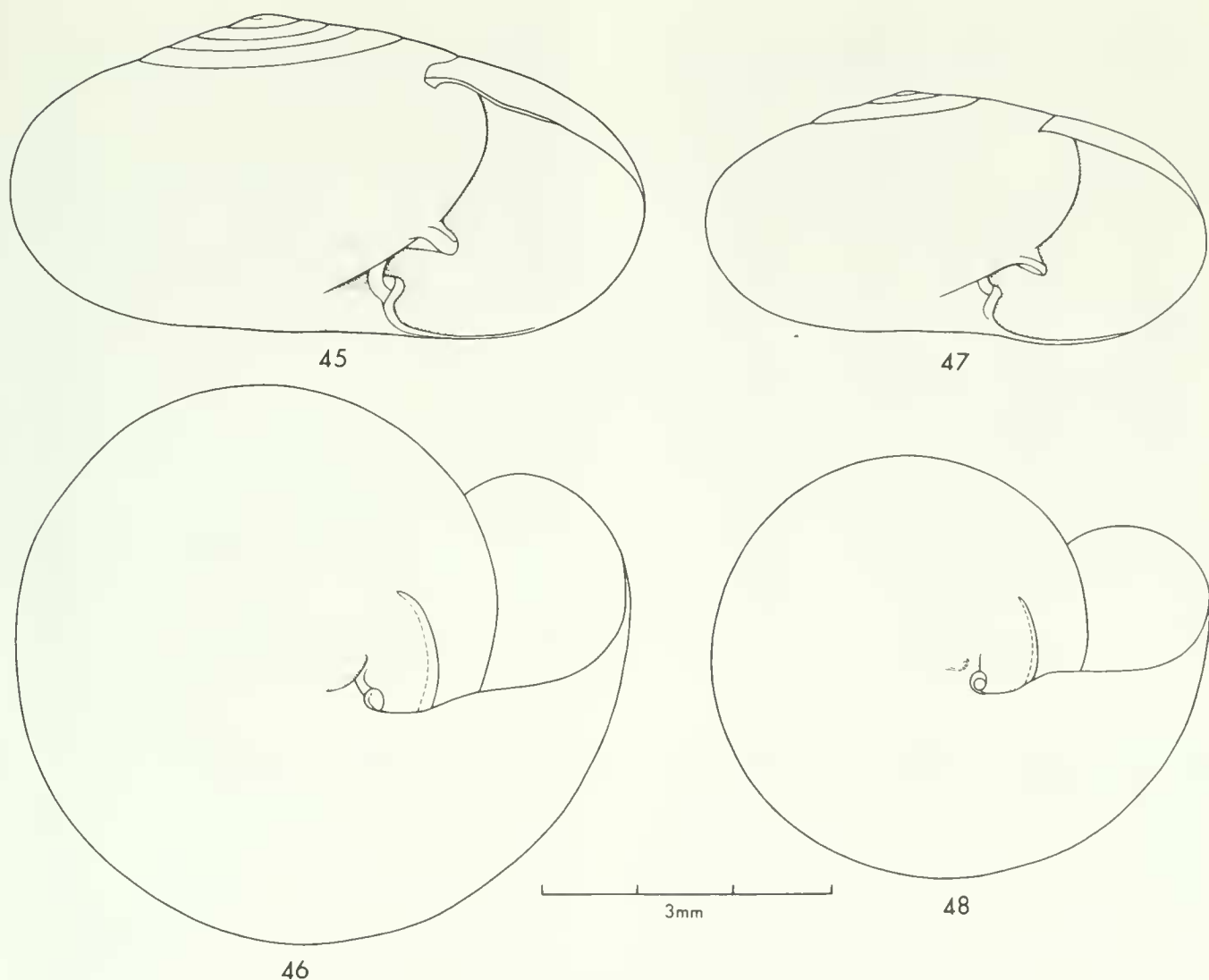
three species groups. One group includes *P. pisum* C. B. Adams from Jamaica and *P. globulosa* (Orbigny) from Cuba. They look alike in having globose or subglobose shells (see Boss & Jacobson, 1975a). These two species need not be considered further for comparison with *P. scudderæ* because of their shapes. The second species group includes *P. depressa* (Orbigny) from Cuba, *P. bidentata* C. B. Adams from Jamaica, and *P. marcanoi* Clench. They are alike in having depressed helicoid shells. Differentiation within this group is slight. *P. depressa* differs by its larger size. Adults attain a diameter of about 7–8 mm. *P. bidentata* and *P. marcanoi* reach a diameter of about 5 mm. *P. bidentata* and *P. marcanoi* are hardly separable. *P. bidentata* has a weaker indentation at the base of the columella than does *P. marcanoi* but other shell differences are nonexistent. They are treated as distinct species because they occur on different islands (Boss & Jacobson, 1975a). A third species group includes *P. scudderæ* and *P. planior* from Hispaniola which differ from other *Despoenella* by

their discoidal shape, with a height/width ratio of less than 0.50, and having protruding embryonic whorls. (See Figs. 42–44 for comparisons with *marcanoi*, Figs. 47–48 for *bidentata*, and Figs. 45–46 for *depressa*.)

*Proserpina marcanoi*, *P. scudderæ*, and *P. planior* are found in Hispaniola. Each is highly restricted in its geographical distribution. *P. marcanoi* is known only from its type-locality, Colonia Majagual, San Cristobal Prov., Dominican Republic (formerly known as Colonia Ramfis). This is a small community located on the road from Gambito Garabitos to El Guineo, and is about 12 km NW of Gambito Garabitos. The area is mountainous and formerly was covered with wet forest which is replaced with coffee groves. The substrate consists primarily of metamorphic and igneous rocks. There are a few isolated outcrops of highly metamorphosed limestones. *P. marcanoi* is known only from the three specimens that comprise the type series. I visited the region of its type-locality on four occasions and was unsuccessful in finding additional specimens. *P. scudderæ* is



FIGS. 42–44. *Proserpina (Despoenella) marcanoi* Clench (Holotype: MCZ 188911).



FIGS. 45–46. *Proserpina (Despoenella) depressa* (Orbigny) (UF 24115).

FIGS. 47–48. *Proserpina (Despoenella) bidentata* (C. B. Adams) (UF 24114).

known only from the immediate vicinity of Polo, Sierra de Baoruco, Barahona Prov., Dominican Republic. *P. planior* is restricted to the Plateau de Rochellois on the Tiburon Peninsula of Haiti. The area formerly was covered with wet forests on a limestone substrate, but is now reduced to vegetable gardens and a few isolated thickets of brush on limestone outcrops.

The extremely isolated and disjunct ranges of these species indicate relictual distributions for the genus on Hispaniola. Each species is confined to a small geographic area, lying at higher, relatively cool and moist elevations on limestone substrates. I have collected at many other places on Hispaniola that would seemingly comprise suitable habitats for proserpinids, but have not found other populations, in contrast to my experience in Jamaica (1976) where I found proserpinids common in occurrence. Possibly other species occur on Hispaniola, but their discovery will be extremely fortuitous!

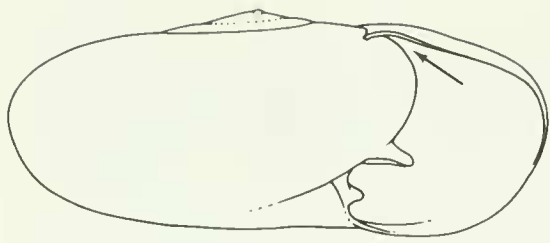
*Proserpina (Despoenella) planior* Thompson,  
new species

*Etymology*: *planior*: from the Latin, *planus*, meaning more flattened, alluding to the distinctive shape of this species compared to other *Proserpina*.

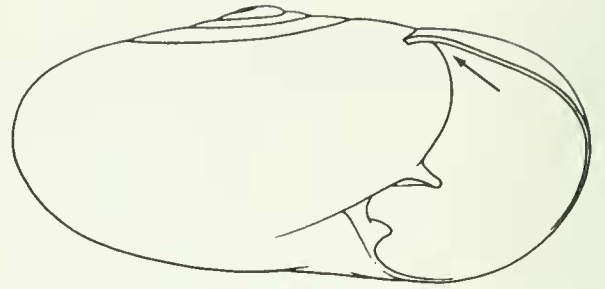
*Type-locality*: Haiti, Departement du Sud, Plateau de Rochellois, 22 km SW Miragoâne, 930 m alt. Holotype: UF 26566, collected 31 March 1979 by Fred G. Thompson and Richard Franz; Paratypes: UF 26565 (6); same data as holotype; UF 26564 (10), collected at type-locality 12 May 1979 by Fred G. Thompson and Kurt Auffenberg.

The type-locality is on the south slope of a small knoll covered by a dense thicket of shrubs and small trees. The area once was densely forested but has been cleared for fuel and agriculture. Shells were found among limestone boulders.

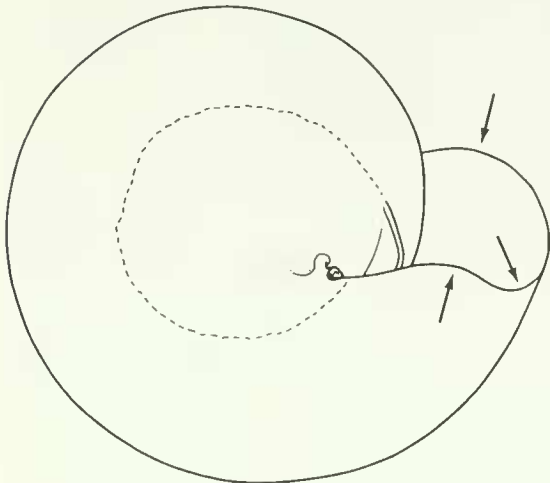
*Shell* (Figs. 49–51): *minute*; adults about 3.8–4.5 mm in diameter. Nearly *planispiral*



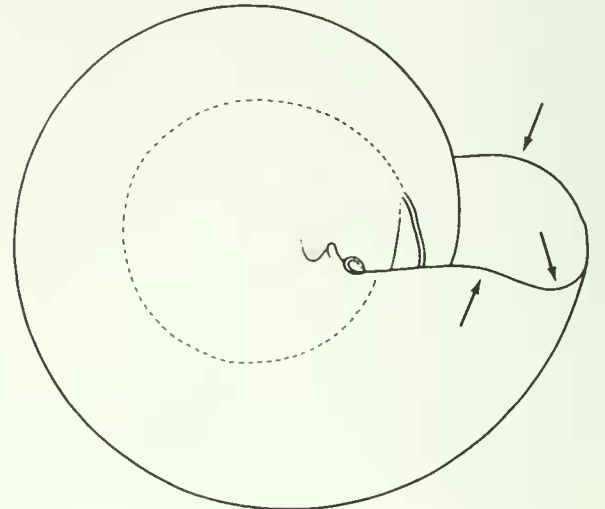
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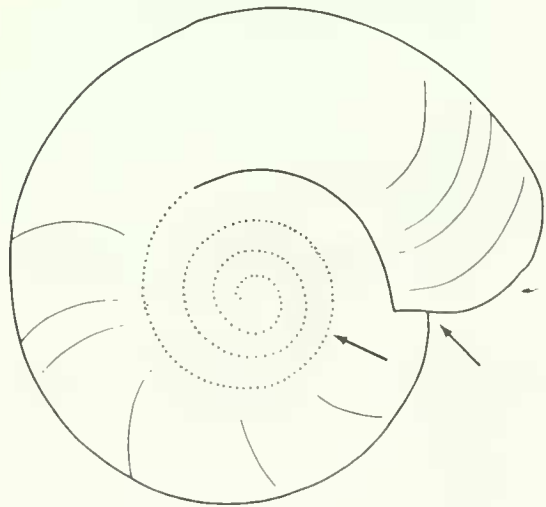
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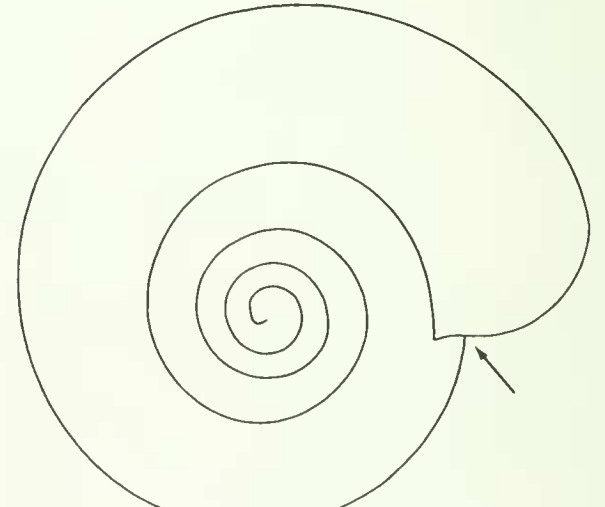
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54



FIGS. 49–51. *Proserpina (Despoenella) planior* new species (Holotype: UF 26566).

FIGS. 52–54. *Proserpina (Despoenella) scudderae* new species (Paratype: UF 24327).

(Fig. 49); 0.42–0.46 times as high as wide; apical whorl slightly elevated as a sharp nipple-like protrusion. Light greenish-yellow when fresh, with a spiral white band on apex due to an internal callus along first 2–3 whorls (Fig. 51). Sides and base thin, subtranspar-

ent. Dorsal surface usually opaque due to internal callus and a relatively thick glassy outer deposit that completely covers previous whorls and obscures sutures. Sutural impression apparent only along last two whorls. About 4.3–4.7 whorls in adult specimens (4.3

in holotype). Surface glossy with a few weak incremental wrinkles. Base with weakly granular circum-umbilical callus. Columellar wall near aperture vertical, forming distinct angle or pit just behind columella (Fig. 50). Aperture bluntly angular at periphery and at basolateral margin; baso-columellar angle more distinct; *posterior angle of dorsal lip very narrow and deep due to high insertion of dorsal lip* which lies about halfway between periphery and sutural impression of previous whorl (Fig. 49). *Peristome strongly arched forward along dorsal lip and relatively deeply receded at suture* (Fig. 51); *lateral lip deeply receded at periphery; basal lip conspicuously arched forward, but not as much as dorsal lip* (Fig. 50). Columella slightly oblique. Interior of aperture with parietal and columellar lamellae. Parietal lamella about  $\frac{1}{3}$  whorl long and located at about  $\frac{1}{3}$  distance from columella to periphery. Columellar lamella about  $\frac{1}{2}$  whorl long and relatively low and thin compared to other species.

Measurements in mm based upon seven specimens to show maximum variation in size (holotype in parenthesis): height 1.75–1.97 (1.82); width 3.78–4.46 (4.35); aperture height, 1.54–1.68 (1.68); aperture width, 1.47–1.75 (1.75).

*Distribution:* known only from the type-locality.

*Remarks:* *P. planior* is most closely related to *P. scudderæ*. The two species are similar to each other and differ from all other *Proserpina* by their depressed shapes and protruding apical whorls. They differ by several consistent characters. An immature paratype of *P. scudderæ* (Figs. 52–54), comparable in diameter and whorl count, is illustrated for comparison to the holotype of *P. planior*. *P. planior* is characterized by its small size, attaining a diameter of 3.8–4.5 mm, by its lower number of whorls, 4.3–4.7, and by its depressed, planular shape, being 0.42–0.46 times as high as wide. The dorsal lip is inserted high on the preceding whorl, about halfway between the periphery and the preceding suture, causing the posterior corner of the aperture to be very narrow and deep. The peristome is strongly sinuous with the dorsal and basal lip strongly arched forward and the outer lip strongly receded. The apex bears a spiral white band and an external callus deposit that completely covers the preceding whorls.

Adult *P. scudderæ* are 4.2–5.9 mm in diameter, have 4.5–5.0 whorls and are 0.47–

0.49 times as high as wide. The dorsal lip is inserted about  $\frac{1}{3}$  the distance from the periphery to the suture, causing the posterior angle of the aperture to be broader and shallower. The peristome is not as strongly curved, the apex is unicolor, and the apical callus overlapping the suture extends only about halfway across the preceding whorls.

It may be argued that *P. planior* and *P. scudderæ* should be treated as subspecies because of their similarities. Such a designation requires evidence that they intergrade, which they do not, either morphologically or geographically. The ranges of the two species are disjunct and are separated by a distance of about 300 km. I have collected at about 200 field stations in the intervening territory and have not encountered other populations of *Proserpina*.

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